

# **Vertical distribution, feeding and migration behaviour of the myctophiid *Benthosema glaciale* in Masfjorden, western Norway**

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## Abstract

This study addresses the mesopelagic fish, *Benthosema glaciale* focusing on feeding, vertical distributions and diel migration pattern. During a cruise with the vessel “Trygve Braarud” to Masfjorden, ~50 km north of Bergen (60°52’30 N, 5°24’70 E) from the 2<sup>nd</sup> to the 6<sup>th</sup> October 2006 fish were sampled by oblique and horizontal trawls. A bottom deployed 38 kHz split beam echosounder, placed at 400 m depth, provided continuous acoustic data on both population and individual level. Mesozooplankton (potential prey) were sampled by net tows and the physical oceanography by CTD and a current meter.

The main population of *B. glaciale* occurred at daytime in a weak back-scattering layer at 180-230 m. At night, peaks in concentrations were found at 0-100 m and in the scattering layer located at 230-270 m. Solitary individuals in a state of low activity were observed at 300-400 m at all times. No evidence of asynchronous diel migration pattern was found and it appears that individuals of *B. glaciale* are switching between performing a diel vertical migration or remain at depth even at night.

During daytime young individuals occurred higher up in the water column with older individuals staying deeper. This was suggested both by oblique trawl sampling, and by sequential horizontal tows made in upper layers at sunset, showing that small specimens were the first to appear in near-surface waters during diel vertical migration.

*Benthosema glaciale* were mainly feeding of copepods and in particular *Calanus sp.* but also on euphausiids, sergestiid shrimps and ostracods. Evidence of both day and night feeding was found but most stomachs examined had very little content, often much digested. No difference was observed in fullness and digestive state between migrants and non-migrants.

Acoustic target tracking showed that the target strength varied from -70 dB to -50 dB for the group ascribed as mesopelagic fish, with a peak at -60 dB corresponding to

fish with a length of 6 cm. The majority of the tracks were long lasting and had little or no speed. Four tracks were studied in more detail. The individual swimming speed was low, yet with frequent changes in speed usually including a rapid shift in vertical position. Such intermittent changes in vertical position were also seen in echograms at 300-400 m. The behaviour may represent a saltatory search behaviour, in which pauses to search for prey alternate with reposition of the predator for scanning new territory.

During the study, the hydrography was vertically homogeneous below the sill and no currents were recorded at depth, suggesting that the results on vertical distribution, swimming speeds and behaviour in the deep part of the water column were not affected by these physical variables.

# 1. Introduction

Fish in the mesopelagic zone, which is defined as depths between 200-1000 m, play an important role in pelagic ecosystem by acting both as a predator on zooplankton and as prey for larger fish. Their migratory and feeding behaviour supports a “biological pump” transporting organic matter between upper and mesopelagic layers (Radchenko, 2007). The family Myctophidae is a worldwide distributed family of mesopelagic fish (Nelson, 2006) and a vital link in the oceans food web.

Myctophiids forage on a diversity of plankton prey, and are themselves preyed upon by a variety of commercial fishes, but also fur seals and cetaceans (Nafpaktitis et al., 1977).

The glacier lanternfish, *Benthosema glaciale* (Reinhart) is a small myctophiid, spawning from the age of 2-3 and seldom reaching the maximum age and size of 8 years and 10.3 cm (Halliday, 1970). It is the most abundant species of the family Myctophidae in the Atlantic, north of ~35° N, and is distributed from Davis straight and southern Baffin Bay to Cape Hatteras in the west and from ~80 N off Svalbard to Cape Verde Island in the east (Gjøsæter, 1973a). Together with Müllers pearlside, *Maurolicus muelleri*, it is the dominating planktivorous mesopelagic fish in the deep, Norwegian fjords (Kristoffersen, 1999; Salvanes, 2001; Aksnes et al., 2004, 2006).

*Benthosema glaciale* feeds mainly on calanoid copepods, but also on euphausiids (Nafpaktitis et al., 1977). It is known to exert a heavy predation pressure on overwintering *Calanus* in Norwegian fjords (Bagøien et al., 2001). In northeast Atlantic *B. glaciale* are preyed upon by e.g. mackerel, *Scomber scombrus*, saithe (*Pollachius virens*) and salmon (*Salmo salar*) (Greer et al., 1993, Salvanes, 2004) and even by birds such as Atlantic puffins (Falk et al., 1992). In Norwegian fjords the larger fish saithe, *Pollachius virens*, and blue whiting, *Micromesistius poutassou*, are common predators (Giske et al., 1990).

Mesopelagic fish perform diel vertical migrations (DVM), a behavioural trait they share with species from various taxa. In the open pelagic environment the deeper and

darker waters provide an efficient hiding place for species with visual predators. In the evening, organisms migrate towards the surface in shelter of darkness to feed in water rich with prey. Hence, diel vertical migration is a trade-off between foraging and predator avoidance. The extent, intensity, and patterns of migration vary between species, but also within a species related to age, or size, and with season and environmental conditions (Pearre, 2003).

Although the hypothesis of a trade-off between foraging and predator avoidance as the main cause of DVM behaviour is widely accepted, the temperature may also be essential. The metabolic rate, growth rate, digestion rate and the energy cost of swimming increase with increasing temperature (Jobling, 1981). Some researchers suggested that intermittent use of cold water, as an energy-conserving mechanism is a causal factor in vertical migration behaviour (Mclaren, 1963; Brett, 1971; Sogard & Olla, 1996). Sogard & Olla (1996) suggested that when the food is scarce, fish will return to colder waters after feeding to lower the cost of metabolism, thereby conserving energy. When food is abundant, the exploitation of thermal gradients can be used to maximize the energy intake as proposed by Wayne & Neverman (1988). Fish ascend to warmer water to stimulate digestion, thereby allowing greater feeding and growth. This advantage is greater than the cost of swimming in higher temperatures.

In Norwegian fjords the main population of *Benthosema glaciale* is distributed below 200 m during the day. During the night *B. glaciale* occurs throughout the water column, with the main population found above 200 m (Gjøsæter, 1973a; Kaartvedt et al., 1988; Bagøien et al., 2001). In other words, most individuals perform a DVM while others may choose to remain at depth; or individuals of *B. glaciale* may migrate at different times of the night, having an asynchronous migration pattern.

The population of *B. glaciale* may have an age structured vertical distribution. In Masfjorden this has been observed during the day in the population of *Maurolicus muelleri* (Giske et al., 1990) with smaller individuals found in the upper regions and older individuals deeper. For young individuals, foraging and growth is of priority



rather than predator avoidance allowing them to take higher risks of predation (Giske et al., 1992).

In this study, I address the vertical distribution, feeding and behaviour of *Benthosema glaciale* in Masfjorden, western Norway. The study is based on sampling and acoustic records during a sampling campaign in autumn. Scientific split-beam echosounders can be used to study both the population migration behaviour, as well as individual swimming behaviour *in situ* (e.g. Torgersen & Kaartvedt, 2001; Klejver & Kaartvedt, 2003). In this study, an echosounder was deployed on the bottom, providing high quality data on deep living individuals in addition to vertical distribution and migration behaviour.

The aim of this study is to provide knowledge of *B. glaciale* on population and individual level during a 24 h time scale. It will focus on:

1. Vertical distribution and migration behaviour
2. Length distribution.
3. Feeding ecology.
4. Individual swimming velocity and behaviour in the lower part of the water column.

## 2. Methods

### 2.1 Study area

The study was carried out from the 2<sup>nd</sup> -5<sup>th</sup> October 2006 in Masfjorden with the research vessel “*Trygve Braarud*”. Masfjorden is located on the west coast of Norway, ~50 km north of Bergen (60°52’30 N, 5°24’70 E). The fjord borders on the larger Fensfjorden, from which it is separated by a 75 m deep sill. Fensfjorden is connected to outer coastal waters. Masfjorden is 20 km long and approximately 1 km wide. It has 2 shallower basins and one deeper, middle basin with a maximum depth of 494 m with average depth of ~430 m.

During the study period fish were sampled by trawling, and net tows were used for assessing distribution of zooplankton (prey). Sampling was carried out in the deeper, middle basin in 5 depth sections; 0-50 m, 50-100 m, 100-200 m, 200-300 m, 300-400 m. A bottom deployed echo sounder, placed at 400 m depth in the middle basin, provided acoustic data during the whole time period. In addition, currents, temperature and salinity were measured.

### 2.2 CTD and current measurements

Salinity and temperature were recorded with a CTD from Falmouth Scientific Inc. The measurement was carried out in the deepest part of the fjord.

A MINI current meter, model SD-6000 recorded currents at ~ 398 m depth. It was placed 10 m from the transducer (2.7 Acoustic instrumental set-up) and was attached to the transceiver cable by a rope and kept suspended by a buoy. It measured currents with speeds stronger than  $1.0 \text{ cm s}^{-1}$ . If the current were weaker the meter shows a current of  $1.0 \text{ cm s}^{-1}$ .

## 2.3 Sampling of mesozooplankton

Mesozooplankton was collected with a WP-2 net with mesh size 200  $\mu\text{m}$ . The net was hauled vertically at  $0.5 \text{ m s}^{-1}$  and closed with Nansen releaser activated by a drop messenger. Filtered volumes were estimated by multiplying towing distance with net aperture ( $\pi r^2$ ,  $r = 0.285 \text{ m}$ ). Duplicate series were taken in five depth sections.

The samples were stored in 4 % neutralised formaldehyde and analysed at University of Oslo, UiO. Large copepods (*Calanus* spp., *Chiridius* spp., *Metridia* spp.) were counted in the samples and identified to genus. The samples were then split in 10 by a LEA plankton divider (Wiborg, 1951). One tenth was analysed with all other copepods being counted and identified, if possible, to genus.

Leica Wild stereomicroscope M8 (ocular Wild 44511, 8-16 x) was used for the analysis.

## 2.4 Trawls

Trawling was carried out with a pelagic trawl equipped with a multisampler opening/closing codend permitting sampling in discrete depth intervals. The trawl has an aperture of  $100 \text{ m}^2$ , and mesh size near the opening was 20 cm declining to 1 cm near the codend. The nets of the multisampler codend were opened and closed by a remote communication and monitoring system (Scanmar HCL hydroacoustic two-way communication link) making it possible to take 3 samples at different depth section in the same tow.

Replicated oblique tows were made in 5 depth intervals during day and night. The day trawls were carried out in a time period from 12:00 h to 16:00 h and the night trawls from 20:30 h to 22:30 h.

To assess the sequence and timing of arrival of species and size groups to upper layers in the evening, horizontal trawling were carried out at the 5<sup>th</sup> October at 60 m depth in the time period from 19:00 h to 21:00 h (apparent sunset occurred at 18:58, local)

Each net was open for approximately 15 minutes and totally 5 sequential samples were obtained.

The trawl catches were handled immediately on deck. The catch was sorted into species and the total weight of each species and the number of individuals was noted. Subsamples were taken on 4 occasions due to large a catch or time limitation. The specimens were frozen and brought to UiO. A subsample of *B. glaciale* from each tow was frozen separately for stomach analysis and length distribution.

The water volume filtered by the trawls was estimated by multiplying the aperture of the trawl by the average towing speed (2 knots) and duration of the trawl.

Jellyfish were not quantified but their occurrence in the trawl was noted.

## 2.5 Length distribution

A subsample of 100 (when available) randomly chosen individuals of *B. glaciale* from each sample was used for establishing length distributions. Fish from the oblique tows were measured immediately on deck. Fish from horizontal tows were measured and weighed after defrosting at UiO.

Each individual was weighted and measured to standard length. The standard length is defined from the most anterior tip of the body to the midlateral posterior edge of the hypural plate (in fish with a hypural plate) or to the posterior end of the vertebral column in fish lacking hypural plates ([www.fishbase.org](http://www.fishbase.org)). The average length and standard deviation was calculated for each depth interval during day and night and for the horizontal tows alone.

## 2.6 Stomach analysis

A subsample of 30 (when available) of randomly chosen individuals from each sample was used for stomach analysis. A total of 505 fish stomachs were examined. The analysis was carried at UiO.

The subsamples were frozen directly after trawling and stored at -18 °C. Before analysis, they were only partly defrosted to a point when dissection was possible to prevent decomposition. The fish were kept in a cold room while waiting to be dissected. The standard length and weight of each fish were measured before dissection. The stomach was taken out by cutting at the anterior end of the oesophagus and at the pyloric valve. The oesophagus was removed together with the stomach to prevent the content from being lost during dissection. The degree of stomach fullness and state of digestion was given a number from 1 to 3 using the categories described in table 1. The stomach contents were flushed into a Petri dish and was analysed to lowest systematic level possible. Leica Wild stereomicroscope M8 (ocular Wild 44511, 8-40 x) was used for the analysis.

**Table 1.** Description the different categories used in stomach fullness and state of digestion.

Category	Stomach fullness	State of digestion
1	Full	Fresh content, species identification is possible.
2	Half full	Partly digested, content can be identified to systematic groups.
3	Empty or very little content	Much digested

## 2.7 Acoustic instrumental set-up

An upward facing 38 kHz split-beam transducer (SIMRAD EKS38DD (7.1°) 38 kHz) was deployed at 400 m depth from the 3<sup>rd</sup> to 6<sup>th</sup> October. The transducer is liquid filled and pressure proof to 1500 m. It was mounted to a steel frame with gimbal couplings to ensure horizontal orientation of the transducer surface (Fig. 2.7.1). It was connected to a Simrad EK60 GPT, general purpose transceiver, which was mounted next to the transducer in a round pressure proof casing, made of glass. The transceiver sent digitized data through an 800 m long cable to a shore-based computer where all

data were stored. The system ran on a 12 V car battery connected to a 220 V transformer to get sufficient voltage for supply through the 800 m of cable. The electrical source caused some noise, apparent as parallel lines in the echograms.



**Figure 2.7.1.** The echo sounder attached to the steel frame with gimbal couplings. The transceiver is placed in a round pressure casing attached next to the transducer.

## 2.8 Acoustic data analysis

The acoustical analysis was carried out by using the software Sonar5\_pro version 5.9.7 (Balk & Lindem, 2007). The data consisted of a total of 39 files from the 3<sup>rd</sup> to the 6<sup>th</sup> October. All files were viewed and no apparent difference between days was observed. In order to facilitate the analysis files from 4<sup>th</sup> to 5<sup>th</sup> (46 hours) October were merged, creating a continuous echogram over the whole water column. This file was used in studying diel vertical migration pattern, behaviour of scattering layers and zooming into shorter time-scale and range.

The software makes it possible to adjust the threshold in the echogram and thereby remove low quality echoes, or noise. The threshold used in the echograms was -81 dB to -83 dB.

### 2.8.1 Automatic target tracking

Automatic target tracking was carried out for a 24-hour period, starting 8:00 h the 4<sup>th</sup> October, in the range of 10 – 100 m from the transducer.

As a target moves through the echo beam it reflects a part of the sound signal back to the transducer. The backscattering signal of a target is termed target strength, TS, and is more or less a species-specific proxy for size. The transducer records the position of the target, as it moves through the echo beam, and the specially designed software combines subsequent echoes from the same organisms into tracks, so-called target tracking.

The acoustic data from automatic tracking were used in establishing target strength distribution and swimming velocities. The automatic tracker only uses echoes defined to originate from single targets based on given criteria. In so-called Single Echo Detection (SED) echograms the echoes are presented as points in time and range. Threshold -70 dB was used during the tracking.

The tracker automatically combines echoes into tracks. The tracks were stored with the information of each track that included date and time, track length, missing pings within the track, mean TS, the speed in x,y and z direction and position of centre of the track. The auto tracker includes four elements; track supporter, gating, association and prediction, in which different parameters can be adjusted acting as filters to reduce the possibility of recording non-existent and unwanted tracks.

#### **Track supporter**

The track supporter determines if a track should be deleted as noise or accepted for further evaluation using the parameters *ping gap* and *track length*. Only tracks containing a minimum of 15 pings with maximum 1 ping missing between recorded echoes were stored.

#### **Gating**

The tracker always predicts the next position of the following echo. The tracker is looking for echoes within a certain range, *gate range* from the predicted position. The

default setting for gate range was used; range of gate was 30 cm and within 50 degrees “athwart ship”, Ath (x-axis) and “along ship”, Alo (y-axis). The gate parameters increase for each missing echo, range by 10 cm and angle by 0.1 degrees Ath and Alo.

### **Association**

If more than one echo is found within a gate, the association unit evaluates each echo. The parameters; *ping*, *range*, *Ath*, *Alo* and *TS* are considered by the tracker and their relative importance are decided by numerical values. The best-suited echo is added to the track. The following default association parameter settings were used: ping=50, range=10, Ath=1, Alo=1, TS=1. The tracker will take priority of the next ping over a ping closer in space.

### **Prediction**

The predictor determines the position of the gate. Four different predictors can be selected; zero velocity, weighted mean, linear regression and the Alpha Beta predictor that were used in this study.

The Alpha Beta predictor estimates the smoothed position from the observed and predicted position. The position equations are using a constant *alpha* and *beta* filter. The constant alpha and beta are given a number from 0-1 and represent the importance of the position of the last echo,  $\alpha$ , and the speed of the track,  $\beta$ , in the equations. See Balk & Lindem (2007) for detailed information. The alpha and beta default setting were used;  $\alpha = 0.5$ ,  $\beta = 0.5$ .

### **Datasets and analysis**

In order to study difference in behaviour during 24 hours the stored tracks were divided into 4 datasets representing the time periods Day, Night, Dawn and Dusk. The apparent sunset and sunrise occurred at 19:02 h the 4<sup>th</sup> October and 07:54 h the 5<sup>th</sup> October local time. The data set Dawn covered the time period from 08:00 h to 10:00 h and Dusk from 18:00 h to 20:00 h. The periods were chosen considering the light extinction at 300-400 m and that migrating individuals are assumed to arrive at this depth after sunset. The datasets Day and Night are from 11:00 h to 16:00 h and



23:00-04:00 h, respectively. The short dawn and dusk periods and the gap in time between the datasets are to minimize the possibility of overlap between the potentially migrating and non-migrating individuals.

The computed parameters were imported into Matlab. The speed components were plotted against TS in scatter plots. The absolute average speed and medians were calculated after removing tracks with TS stronger than -45 dB.

### 2.8.2 Analysis of variation within tracks

Variation in position, speed and TS within a track was analysed. Three tracks were chosen and tracked manually. In addition, one track recorded by automatic tracking was used.

The manual target tracking was carried out using an ordinary (amplitude) echogram with a threshold of -78 dB. Manual target tracking are simply done by drawing a rectangle with the mouse around an echo trace, which evidently originates from a single organisms. The tracks chosen were representative in that they were visually very similar to most tracks ascribed as mesopelagic fish. Two tracks close to the transducer, ~15 m, were chosen. The tracks had one missing ping. The third track was 100 m from the transducer with 12 missing ping. The missing pings were interpolated or removed if they occurred at the end or beginning of the track.

The variation in speed within the track was calculated after importing the tracks parameters into Matlab. The speed,  $v$ , was calculated by dividing the Euclidean distance between the echoes (eq. 1, Balk & Lindem, 2007) by the time that had passed (eq. 2, Balk & Lindem, 2007). The time between the echoes was calculated by dividing the number of pings between the echoes by the number of pings per second (0.9496). The calculated speed and the TS variable were smoothed,  $v_s$  and  $TS_s$ , by a running mean. Tracks from manually tracking were smoothed by a 3-point running mean (eq. 3) and in the automatic recorded track by a 5-point running mean.

Equation 1

$$\vec{v} = \frac{\sqrt{(x_{i+1}-x_i)^2 + (y_{i+1}-y_i)^2 + (z_{i+1}-z_i)^2}}{\Delta t}$$

Equation 2

$$\Delta t = \frac{Ping_{i+1} - Ping_i}{0.9496}$$

Equation 3

$$\vec{v}_s = \frac{\vec{v}_i + \vec{v}_{i+1} + \vec{v}_{i+2}}{3}$$

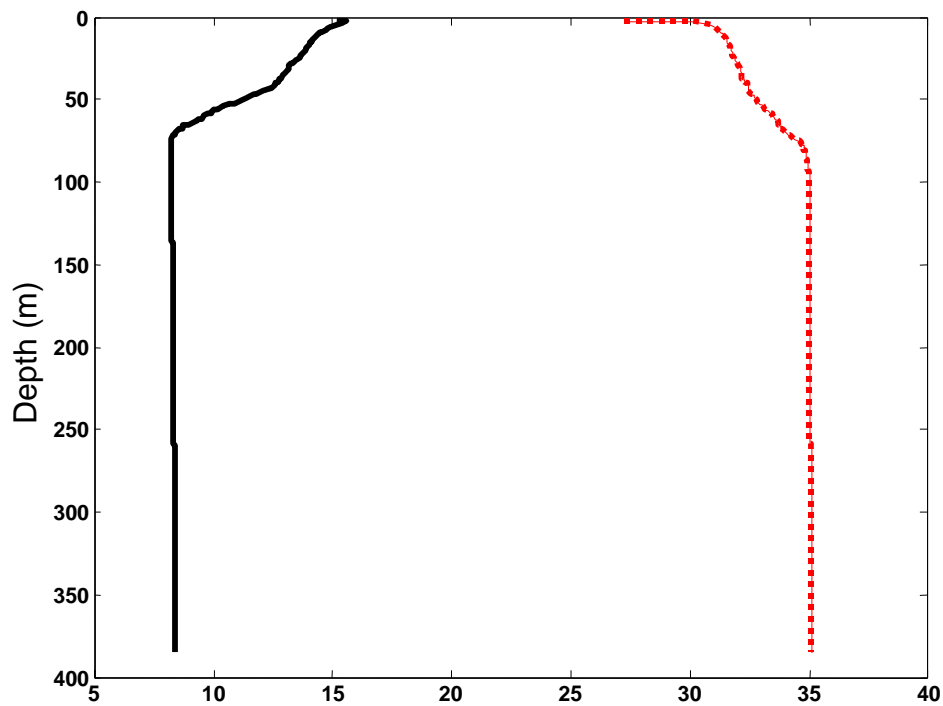
$$TS_s = \frac{TS_i + TS_{i+1} + TS_{i+2}}{3}$$

### 3. Results

#### 3.1 CTD and current measurements

The water column consisted of a warmer and less saline layer, stretching down to 75 m, on top of a uniform water mass (Fig.3.1.1). The temperature had a maximum of 15 °C at 6 m and decreased to 8.5 °C at 75 m. The salinity increased from 22 psu to 35 psu from the surface to 75 m. Both temperature and salinity remained relatively constant below.

The current meter showed a current of  $1.0 \text{ cm s}^{-1}$  during the whole time period.

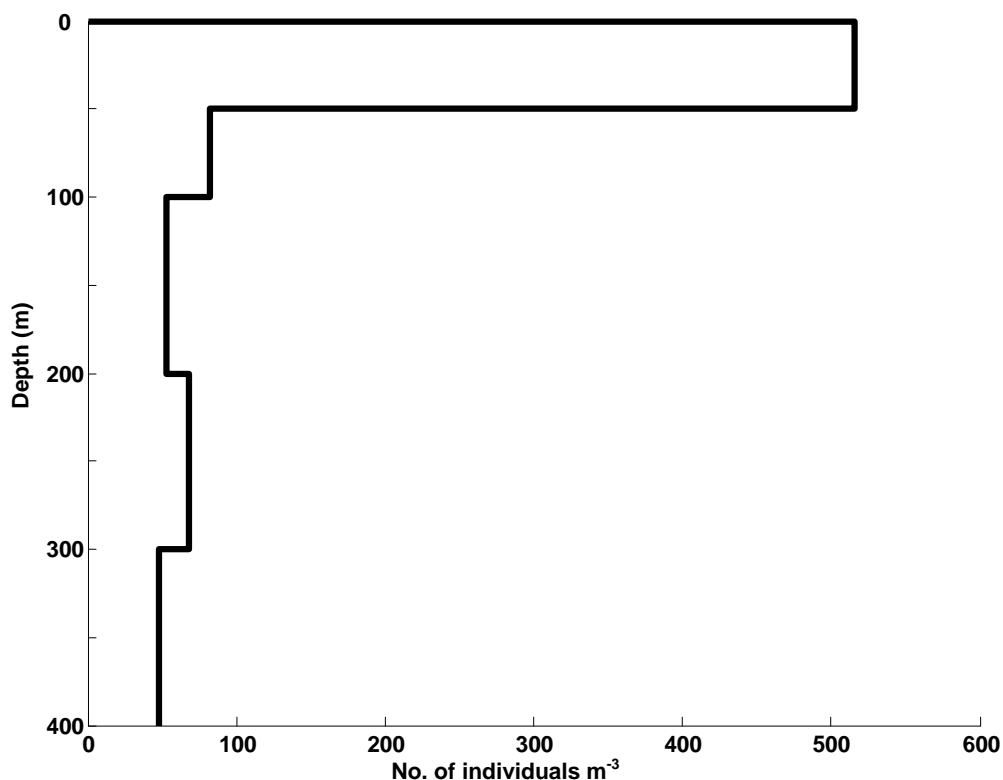


**Figure 3.1.1.** Temperature (-) and salinity (--) profiles as a function of depth.

### 3.2 Vertical distribution of mesozooplankton

Copepods dominated the mesozooplankton samples with the highest concentrations in the upper 50 m (Fig. 3.2.1), and low concentrations of copepods and other zooplanktons below. Smaller copepods prevailed at 0-50 m, the most numerous generally being *Oithona* spp. and *Acartia* spp. (Tab.2). *Oncaea* spp. also occurred in low numbers. The concentration of *Calanus* spp. was highest at 200-300 m (23 ind.  $\text{m}^{-3}$ ) but the overall abundance was low. The larger copepods *Metridia* spp. and *Chiridius* spp. were also recognized in the samples but in low numbers.

A few Ostracoda were collected below 200 m. In addition, some Chaethognatha, cnidarians; siphonophors and ctenophors (*Lensia* spp., *Aglantia digitale*, *Beroe* and Swimming bell) occurred in the samples, below 100 m.



**Figure 3.2.1.** The total number of copepods in the zooplankton samples (number of individuals  $\text{m}^{-3}$ ).

**Table 2.** Number of individuals per m<sup>3</sup> of the different species occurring in the zooplankton sample.

Depth	<i>Calanus</i> spp.	<i>Metridia</i> spp.	<i>Chiridius</i> spp.	<i>Oithona</i> spp.	<i>Oncaea</i> spp.	<i>Acartia</i> spp.	Other copepods	<i>Ostracoda</i>
0-50	13	4	3	129	9	179	179	
50-100	2	2	0	37	2	8	31	
100-200	16	7	0	14	2	6	8	
200-300	23	9	1	14	6	1	13	3
300-400	14	4	1	10	2	1	17	1

### 3.3 Oblique trawl catches

The light fish, *Maurolicus muelleri* was generally numerically dominant over *B. glaciale* in the trawls (Tab. 3). Euphausiids and *Sergestes arcticus* were also common. The shrimp *Pasiphaea spp.* appeared in the trawls in low amount.

The tows < 100 m during the day consisted mostly of *M. muelleri*. At 100-200 m depth, the largest amount of *M. muelleri*, *B. glaciale* and euphausiids were collected. The tows at 200-300 m contained mainly *S. arcticus* and *B. glaciale*. The deepest tows at 300-400 m also contained a significant amount of *M. muelleri* in addition to *S. arcticus* and *B. glaciale*. The proportion of the species in the deeper trawls did not change from day to night.

At night, *M. muelleri* and euphausiids were concentrated at 0-50 m. *S. arcticus* and *B. glaciale* was distributed throughout the water column.

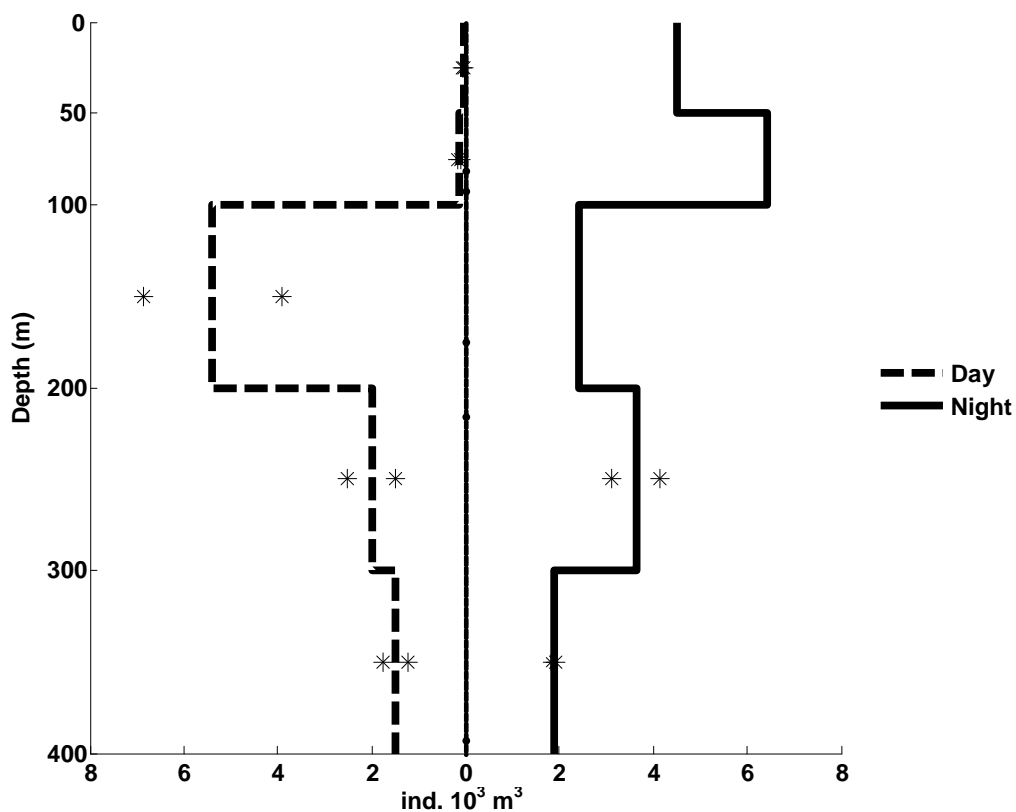
In addition, one *Merlangius merlangus* was collected during day and one *Pollachius virens* collected during night, both at 0-50 m. The ctenophore *Beroe sp.* and siphonophore *Lensia sp.* occurred in all trawls. A few specimens of *Periphylla periphylla* and *Cyanea capillata* were collected.

**Table 3.** The estimated average concentrations (ind.  $10^3 \text{ m}^{-3}$ ) of the species collected by oblique and horizontal trawls.

Day (m)	<i>B. glaciale</i>	<i>M. muelleri</i>	<i>S. arcticus</i>	Euphausiacea	<i>Pasiphaea</i> <i>spp.</i>	Mysidacea	Other fish
0-50	0,1	4,2	0,2	1,1	0	0	1 ind. of <i>Merlangius merlangus</i>
50-100	0,1	16,8	0,9	1,3	0	0	
100-200	5,6	105	6,8	4,8	0	0	
200-300	2,1	0,9	8,5	1,3	0	0,1	
300-400	1,5	3,5	4,9	0,7	0,1	2,1	
<b>Night (m)</b>							
0-50	4,7	10,4	5,8	10,8	0	0,1	1 ind. of <i>Pollachius virens</i>
50-100	6,6	5,7	3,3	3,2	0,1	1,9	
100-200	2,5	3,8	3,9	2,4	0,1	0,7	
200-300	3,7	0,8	5,1	1,3	0	1,7	
300-400	1,9	2,4	4,7	1,2	0,1	0,8	
<b>Hour (60 m)</b>							
18:59-19:18	0	205,9	0	6,8	0	0	
19:22-19:37	0,3	45,3	7	7,8	0	0	
19:41-19:56	3,8	13,4	2,3	2,1	0	0	
20:29-20:45	0,9	24,8	4,3	0,5	0,2	0	1 ind. of <i>Merlangius merlangus</i>
20:47-21:01	0,9	17,4	5,9	0,3	0,2	0,2	1 ind. of <i>Pollachius virens</i>

### 3.4 Vertical distribution of *B. glaciale*

*Benthoosema glaciale* showed a shift in the vertical distribution from day to night (Fig.3.4.1). It was nearly absent above 100 m during day and the highest average concentration was found at 100-200 m, ( $5.6 \text{ ind. } 10^3 \text{ m}^{-3}$ , Tab. 3). During the night, the main concentrations were found above 100 m with a maximum in the depth section from 50-100 m, ( $6.6 \text{ ind. } 10^3 \text{ m}^{-3}$ ). In the 2 deeper depth intervals the average concentrations were as high (or higher) at night ( $3.7$  and  $1.9 \text{ ind. } 10^3 \text{ m}^{-3}$ ) than at day ( $2.1$  and  $1.5 \text{ ind. } 10^3 \text{ m}^{-3}$ ).



**Figure 3.4.1.** The average number of *B. glaciale* (line) during day (left) and night (right) estimated from the replicates (\*). Only one replicate was carried from 0 to 200 m during the night.

## 3.5 Length distribution

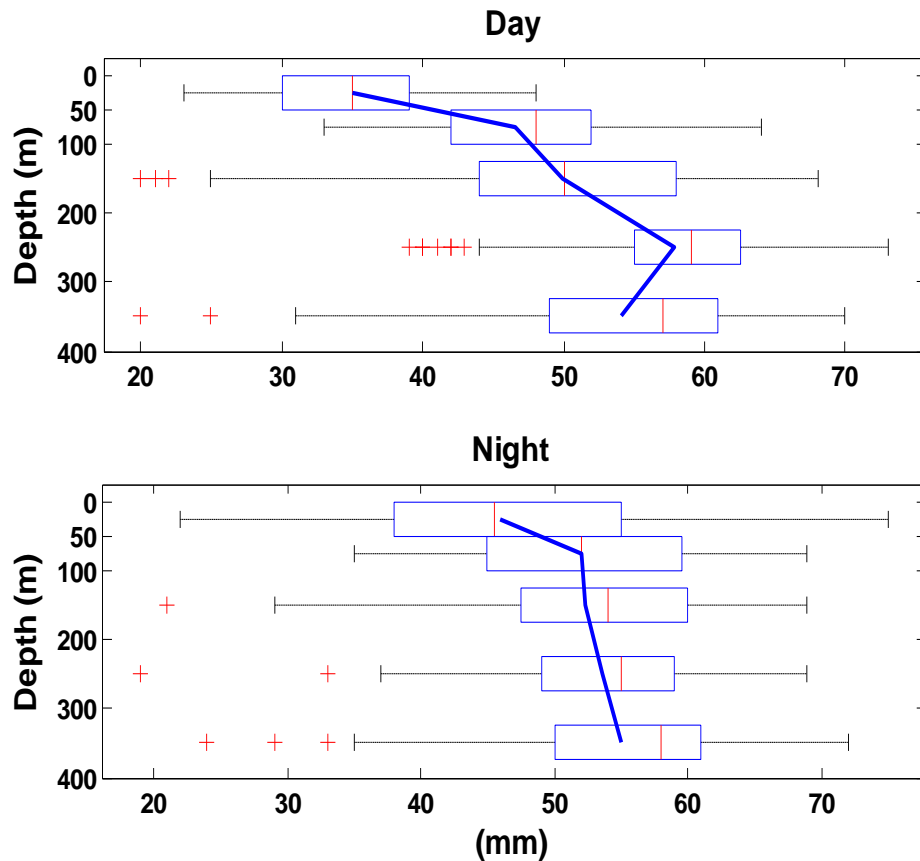
### 3.5.1 Length distribution by depth

There were large variations in length at all depth intervals both day and night. The largest variation was found at 100-200 m during the day and at 0-50 m during the night (Fig. 3.5.1.1), i.e. in the intervals where the concentrations of *B. glaciale* were high.

The average length was lowest at 0-50 m both at day (35 mm) and at night (46 mm). Only 5 fish were collected and measured at 0-50 m during the day and could not be compared statistically to other depth sections. The largest individuals were collected at this depth at night although a low average.

The average length increased with depth during the day to 58 mm at 200-300 m and was slightly lower below (54 mm). There was less variation in average length between the sections during night (46-55) with larger individuals spread out in the water column. The standard deviations (7-11) and boxes in figure 3.5.1.1 were overlapping and no further statistically significant analysis were carried out.

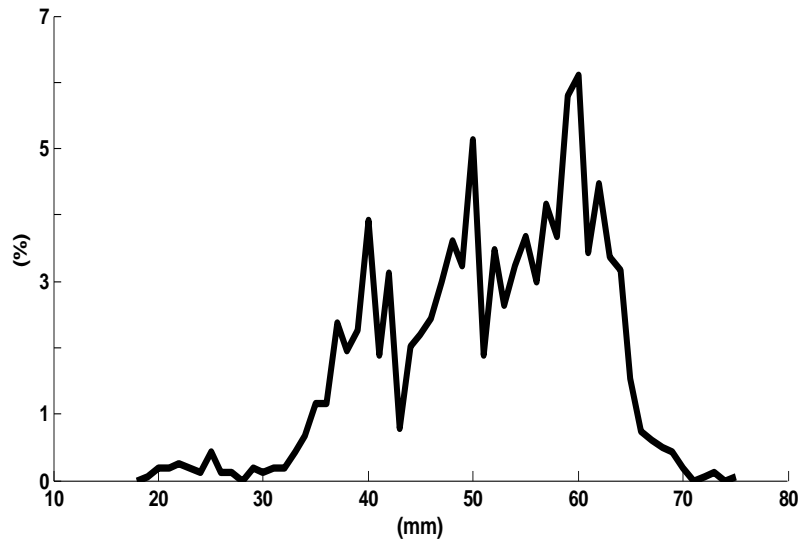




**Figure 3.5.1.1.** Each box shows the average (line) and the range of the length frequencies at each depth interval during day and night. The box shows the lower quartile, median and upper quartile with the lines showing the extent of the rest of the data. Outliers are plotted as crosses.

### 3.5.2 Total length distribution

The length for all fish measured, including those from the horizontal trawls (3.6 Horizontal trawls), varied from 19 mm to 75 mm with peaks at 25, 40, 50 and 60 mm (Fig. 3.5.2.1). The peaks possibly represent different age groups. Smaller fish were less frequent and the highest proportion of fish measured was 50 mm to 65 mm in length. Only a few fish were larger than 65 mm.



**Figure 3.5.2.1.** Length distribution for all the fish measured.

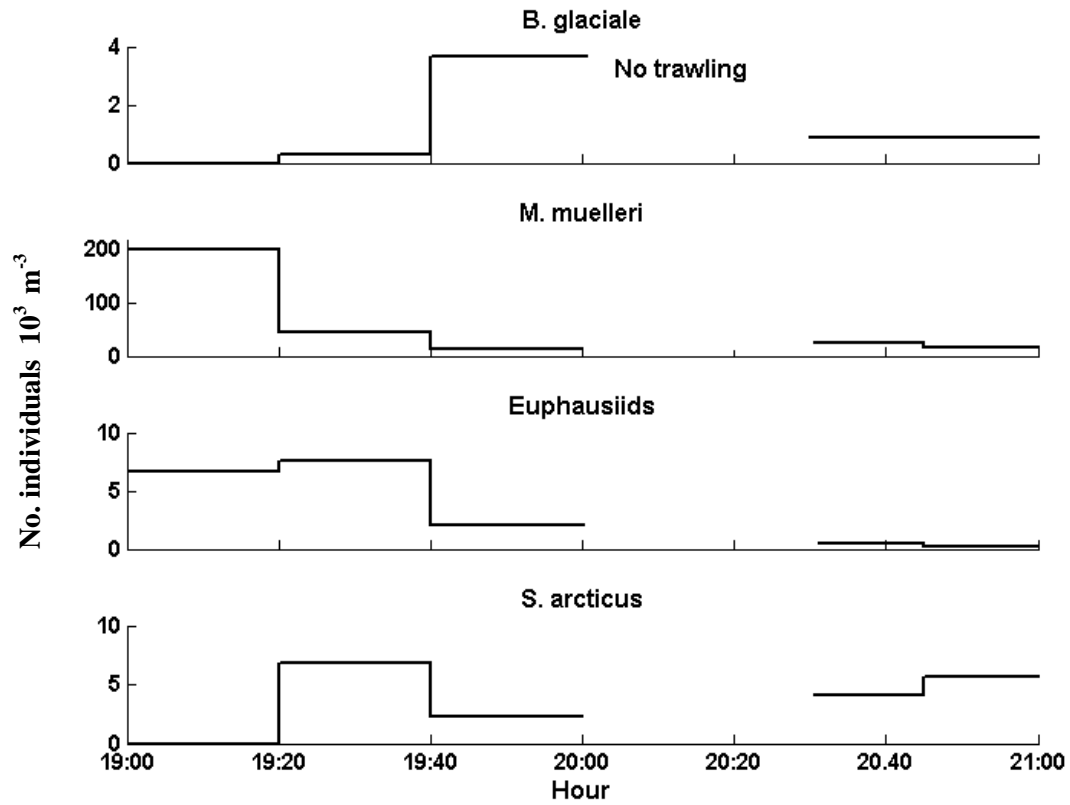
### 3.6 Horizontal trawls

The horizontal trawls revealed a difference in sequence and arrival of species in upper layers. Figure 3.6.1 shows the change in the number of individuals with time for the different species. No trawling was carried out between 20:00 h to 20:30 h.

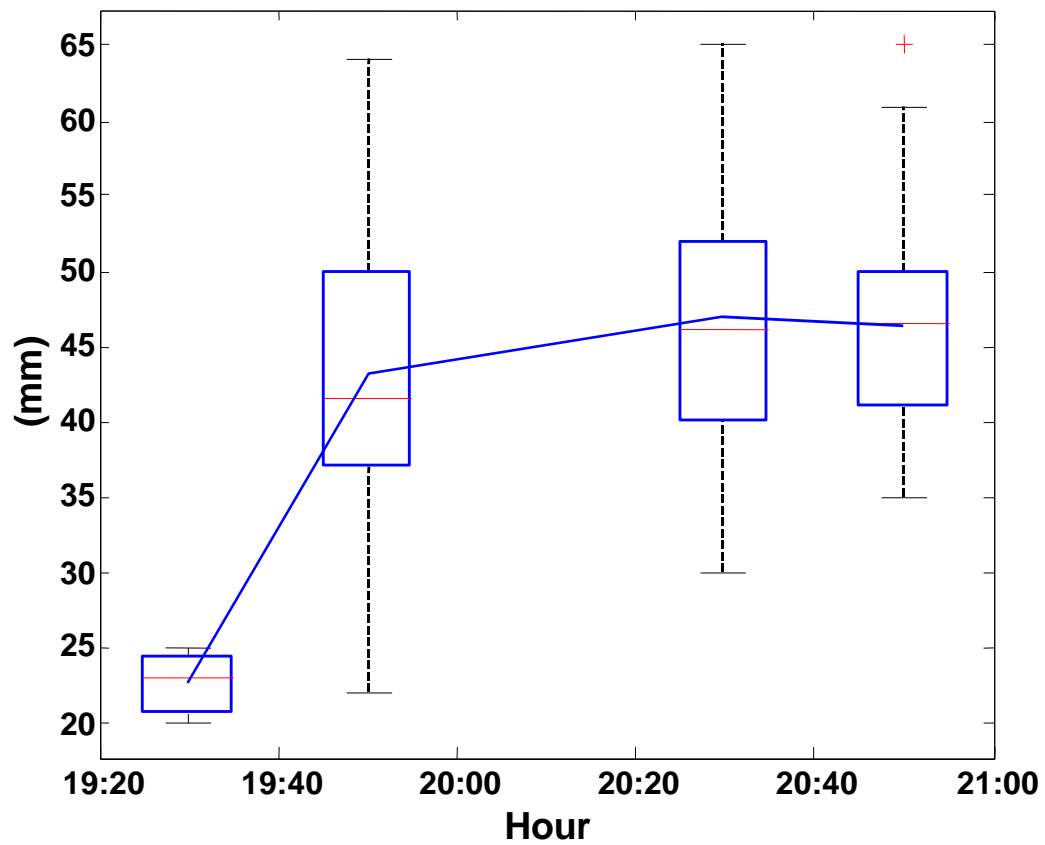
The first tow contained only *M. muelleri* and euphausiids. The number of *M. muelleri* decreased in the second tow, which contained an equal amount of euphausiids as shrimps (Tab. 3). A few, very small, *B. glaciale* appeared at this time. They had an average length of 22.6 mm (standard deviation=2.5 mm, Fig 3.6.2). In the subsequent tow (next 15 minutes), the number of *B. glaciale* increased ten-fold (from 0.3 to 3.8 ind. $\cdot 10^3 \text{ m}^{-3}$ ). This net also held a relatively low number of *M. muelleri*, euphausiids and *S. arcticus*. After the 30-minute period of no trawling, a low number of *B. glaciale*, *M. muelleri* and euphausiids were obtained in the last 2 tows (20:30 h to 21:00 h). Only the amount of *S. arcticus* increased in the last tow. One *Pollachius virens* and one *Merlangius merlangus* was collected in the last 2 tows.

The average length of *B. glaciale* varied little between the last 3 tows (43.2 mm to 46.9 mm, Fig. 3.6.2) with overlapping boxes and standard deviations (6.3-8.7). In the

first tow, only 4 fish were measured and the difference could not be compared statistically with fish from the other tows.



**Figure 3.6.1.** The number of individuals per  $10^3 \text{ m}^3$  (y-axis) of the different species collected by the horizontal trawl at 60 m during a time period from 19:00 h to 21:00 h (x-axis). No trawling was carried out between 20:00-20:30 h.



**Figure 3.6.2.** Each box shows the average (line) and the range of the length frequencies from each tow at 60 m. The box shows the lower quartile, median and upper quartile with the lines showing the extent of the rest of the data. Outliers are plotted as crosses.

## 3.7 Stomach analysis

### 3.7.1 Stomach content

Stomachs, both from fish in oblique and horizontal trawls, often contained a little amount of mostly unidentifiable content. Copepods were the most common prey (Tab. 4, 5) and were often digested to a point where identification to genus was impossible. Of the less digested copepods *Calanus* sp. was most commonly recorded (27 stomachs). The only other copepods recognized were *Chiridus* sp. and *Metridia* sp., which were found in 6 and 8 stomachs respectively. In 2 stomachs were smaller copepods found assuming to be Micro- or Para/Pseudocalanus.

Krill occurred in 28 stomachs, corresponding to 6 %. The shrimp *Sergestes arcticus* and Ostracoda were found in 3 and 4 stomachs respectively.

It was most common with only one type of prey in the stomachs. A few fish had feed both of copepods and euphausiids, or different species of copepods together with ostracods or *S. arcticus*.

**Table 4.** Stomach content, average stomach fullness and state of digestion with standard deviations (std) for every depth section day and night. Unidentified copepods are named as varia.

	Day					Night				
Depth (m)	0-50	50-100	100-200	200-300	300-400	0-50	50-100	100-200	200-300	300-400
n	5	16	60	60	60	30	30	30	60	60
Stomach fullness (std)	2 (0,6)	2 (0,6)	2,7 (0,6)	2,2 (0,7)	2,4 (0,7)	2,4 (0,7)	2,7 (0,5)	2,9 (0,3)	2,4 (0,6)	2,5 (0,7)
State of digestion (std)	2,3 (0,6)	2,1 (1,0)	2,1 (0,7)	2,3 (0,8)	2,5 (0,7)	3,0 (0,2)	2,9 (0,3)	3,0 (0,0)	2,7 (0,6)	2,7 (0,4)
Copepoda, varia	3	2	23	16	10	2	3		5	3
<i>Calanus</i> sp.		4	6	8	5				2	
<i>Metridia</i> sp.				1	2				2	2
<i>Chiridius</i> sp.				1	2				2	
<i>Micro/psuedocalanus</i> sp.		1								
Euphausiacea			1	6	9	1		1	1	8
Sergestes arcticus					2				1	
Ostracoda					1					2
Unidentified	1	8	28	28	29	22	26	21	43	39
Empty	1	1	3	1	3	5	1	8	7	6

**Table 5.** Stomach content and average stomach fullness and state of digestion with standard deviations (std) for the horizontal tows. Unidentified copepods are named as varia.

Hour	19:22-19:37	19:41-19:56	20:29-20:45	20:47-21:01
n	4	30	30	30
Stomach fullness (std)	2,5 (0,6)	2,3 (0,5)	2,6 (0,6)	2,6 (0,5)
State of digestion (std)	2,8 (0,5)	2,5 (0,7)	2,7 (0,5)	2,8 (0,5)
Copepoda, varia	1	6	6	4
<i>Calanus</i> sp.		2		
<i>Metridia</i> sp.		1		
<i>Chiridius</i> sp.		1		
<i>Micro/psuedocalanus</i> sp.				1
Euphausiacea		1		
Sergestes arcticus				
Ostracoda			1	
Unidentified	3	19	19	23
Empty		0	4	3

### 3.7.2 Oblique trawls

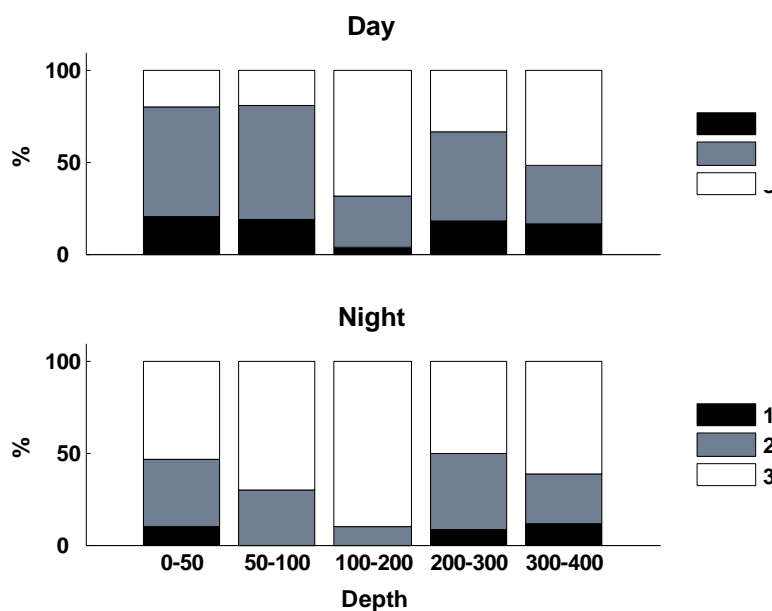
#### *Stomach fullness*

At night > 50% of the stomachs were empty or nearly empty at all depth intervals and few stomachs were full (Fig. 3.7.2.1). The average stomach fullness varied from 2.4-2.9 (Tab. 4). During the day, most stomachs were in category 2 with average fullness from 2-2.7. Full stomachs were found at a higher frequency during the night compared to night at all depths. The highest frequencies of empty stomachs were found at 100-200 m both day and night.

#### *State of digestion*

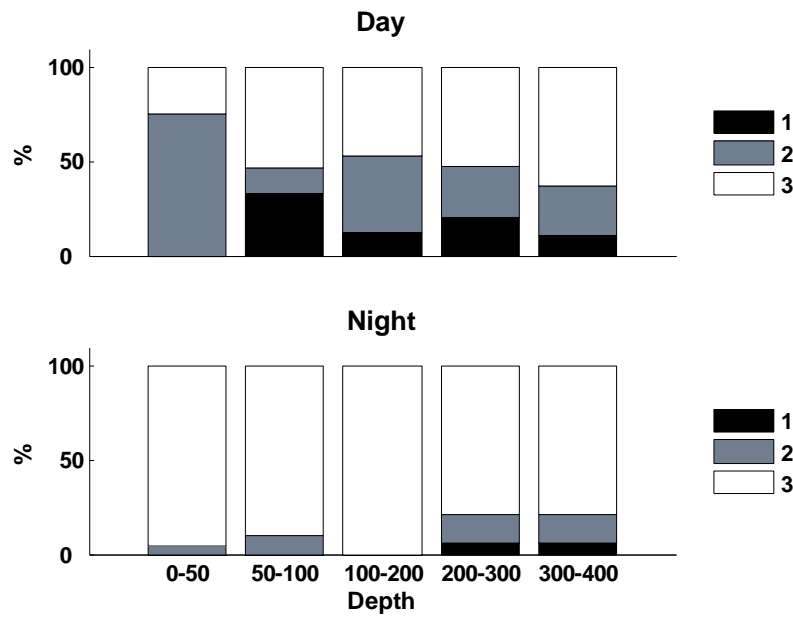
The stomach content was generally partly, or much digested during the day (Fig. 3.7.2.2). The average digestive state varied from 2.1 to 2.5 (Tab. 4). Fresh content were found in 4 depth intervals but were not common.

Nearly all stomachs collected at night contained much digested content. The average digestive state varied from 2.7 to 3. Only a few fish collected at 200-400 m contained fresh content.



**Figure 3.7.2.1.** The frequency of categories; 1= full, 2= half full, 3= empty or very little content, in stomach fullness during day and night at different depths (x-axis).

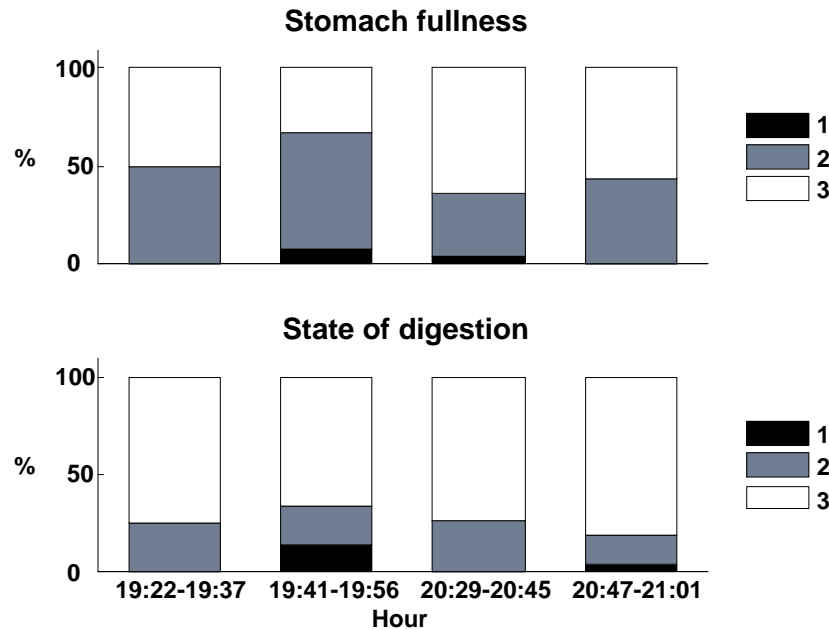




**Figure 3.7.2.2.** The frequency of categories; 1= fresh or nearly fresh, 2=partly digested, 3= much digested.

### 3.7.3 Horizontal trawls

There was little difference with time in fullness and digestive state. During the first time period only 4 fish were analyzed. The 3 later trawls were similar in stomach fullness and digestive state. Fresh stomach content was found in 2 time periods (19:41 h to 19:56 h and 20:47 h to 21:01 h). It was very little difference considering average stomach fullness (2.3-2.6) and state of digestion (2.5-2.8) between the trawls (Tab. 5).



**Figure 3.7.3.1.** The frequency of categories; 1= full, 2= half full, 3= empty or nearly empty, in stomach fullness during day and night at different time (x-axis). The frequency of categories; 1= fresh or nearly fresh, 2= digestion have proceeded, 3 = fully digested (lower figure).

## 3.8 Acoustic analysis

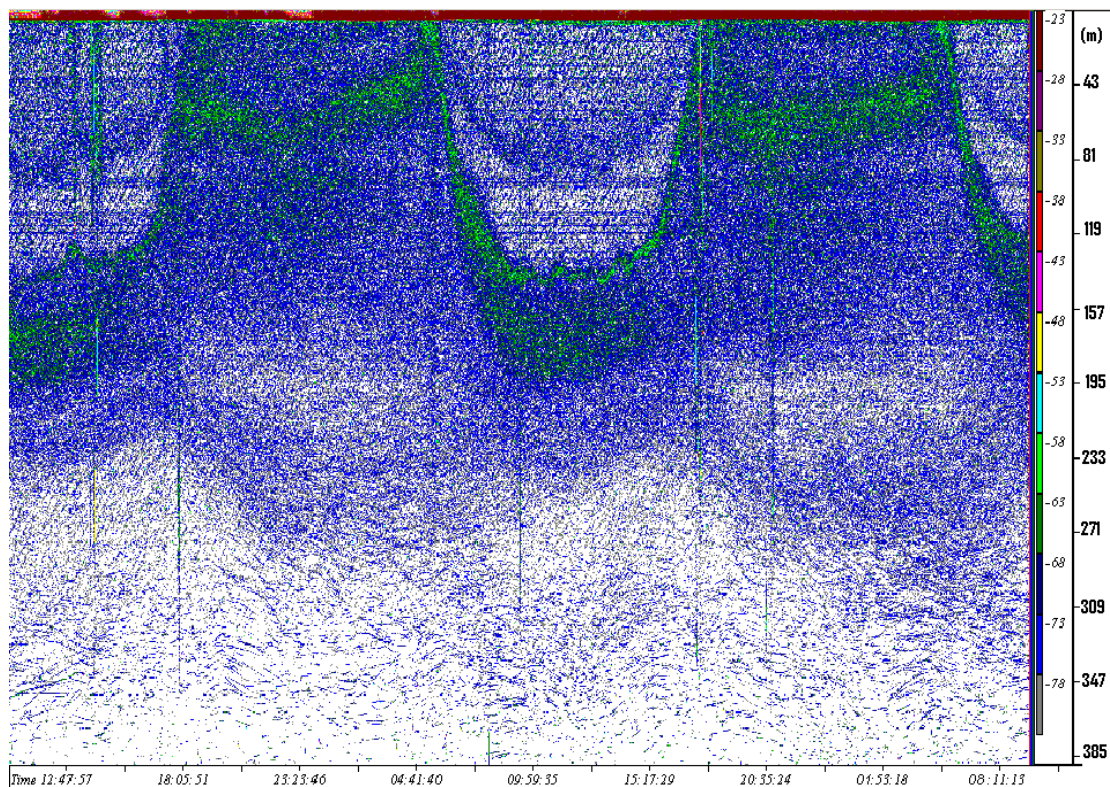
### 3.8.1 Scattering layers

The continuous echogram from the 4<sup>th</sup> (12:12 h) to 6<sup>th</sup> October (10:42 h), shows a sound scattering layer, SL, between ~120-180 m during day (Fig. 3.8.1.1). A second layer with weaker backscatter was located between 180-230 m. The oblique trawl catches show that the upper layer was mainly consisting of *M. muelleri* and euphausiids and the lower layer likely of *B. glaciale* and *S. arcticus*.

The upper layer started to migrate towards surface at approximately 18.45 h. The lower layer had a short rise of ~50 m and sank shortly deeper than the day depth, 230-270. The upward migration coincided with the apparent sunset at 19:02 h. Zooming into a shorter timescale during dusk gives a higher resolution of the separation and migration of the layers (Fig. 3.8.1.2). A part of the migrating layer stayed at ~100 m

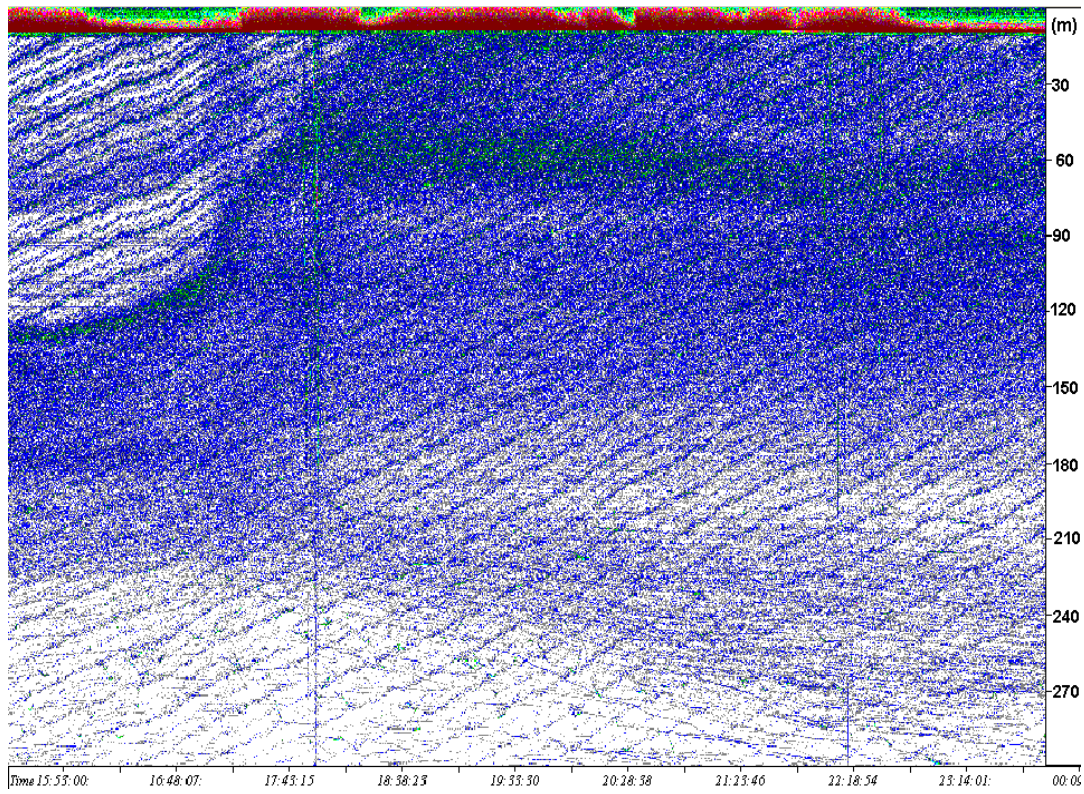
and under the pycnocline at 75 m, while another part migrated closer to surface. The upper SL which reached the surface sank shortly after to ~60 m, where it stayed during the night and rose to the surface again before sunrise (Fig. 3.8.1.1). The downward migration started shortly after the apparent sunrise (~08:00 h). The lower, weak backscattering layer rose to the daytime depth in the morning.

It the lower water column and below the SL's single targets were recorded both day and night (Fig. 3.8.1.3). The majority of the targets had TS of ~60 dB. These targets are ascribed to *B. glaciale* or possibly *M. muelleri*, which also appeared in the trawls. They are further on referred to as mesopelagic fish.

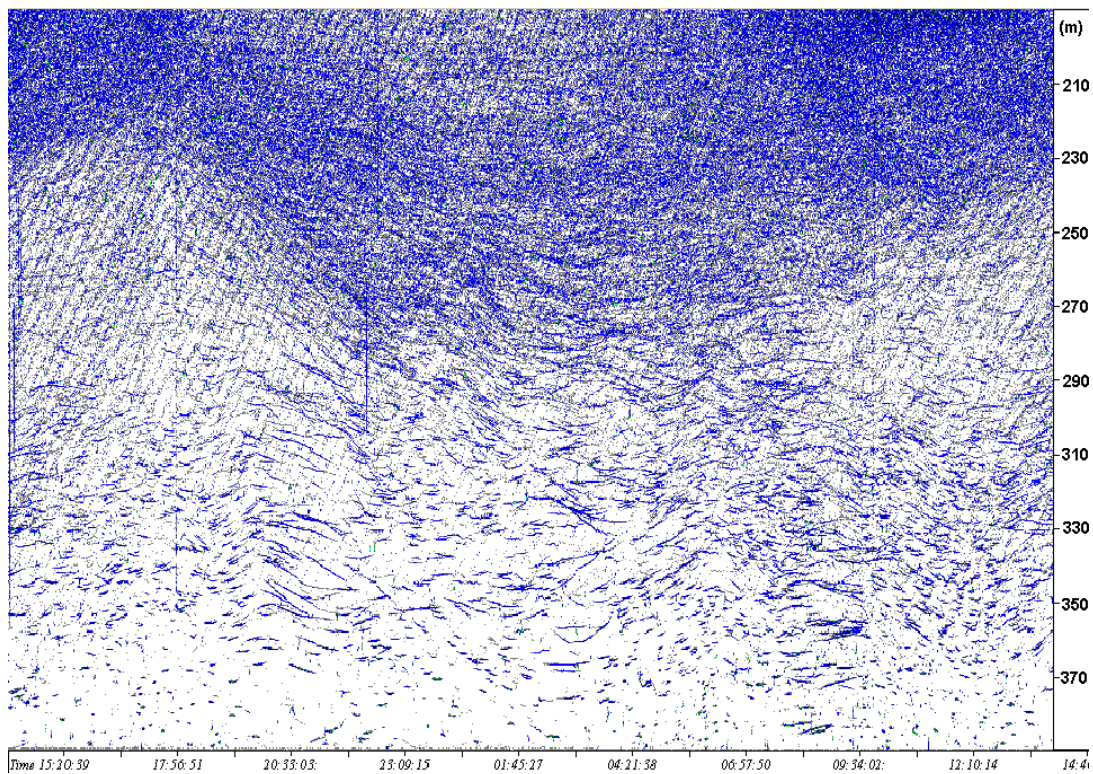


**Figure 3.8.1.1.** Echogram from 4<sup>th</sup> (10:12 h) - 5<sup>th</sup> (08:42 h, GMT) October.





**Figure 4.8.1.2.** Echogram the 4<sup>th</sup> of October from ~15:45 h to 00:00 h (GMT).



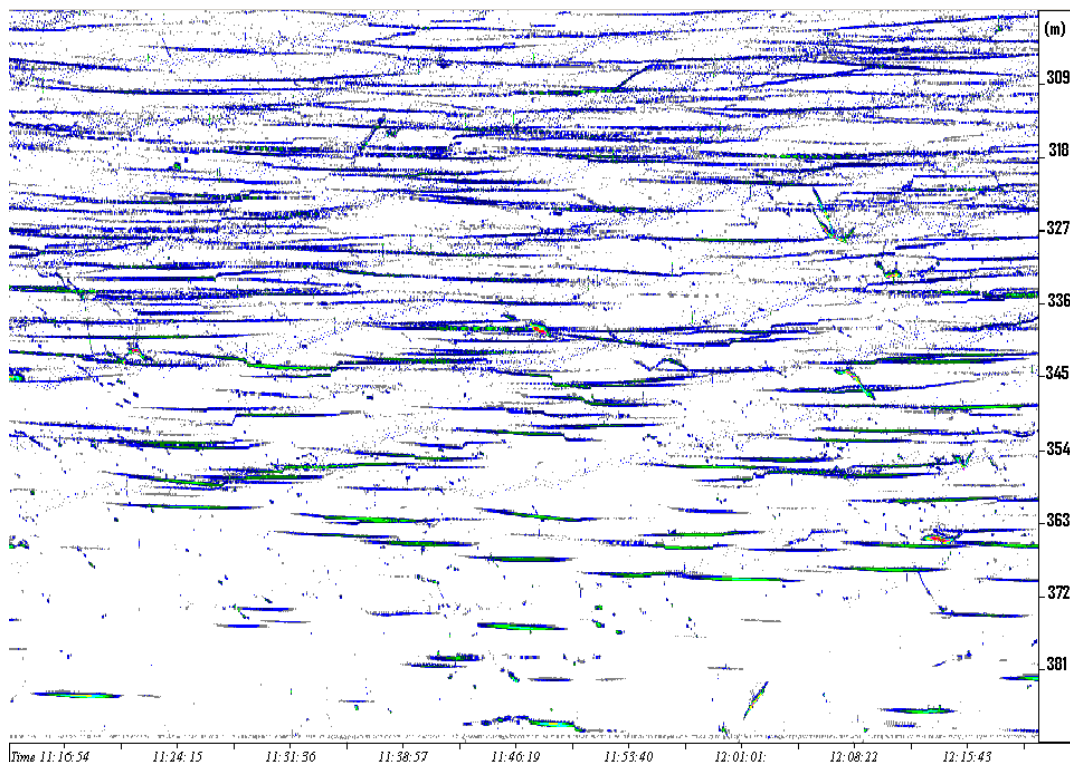
**Figure 3.8.1.3.** Echogram over 24 hours showing the lower part of the water column.



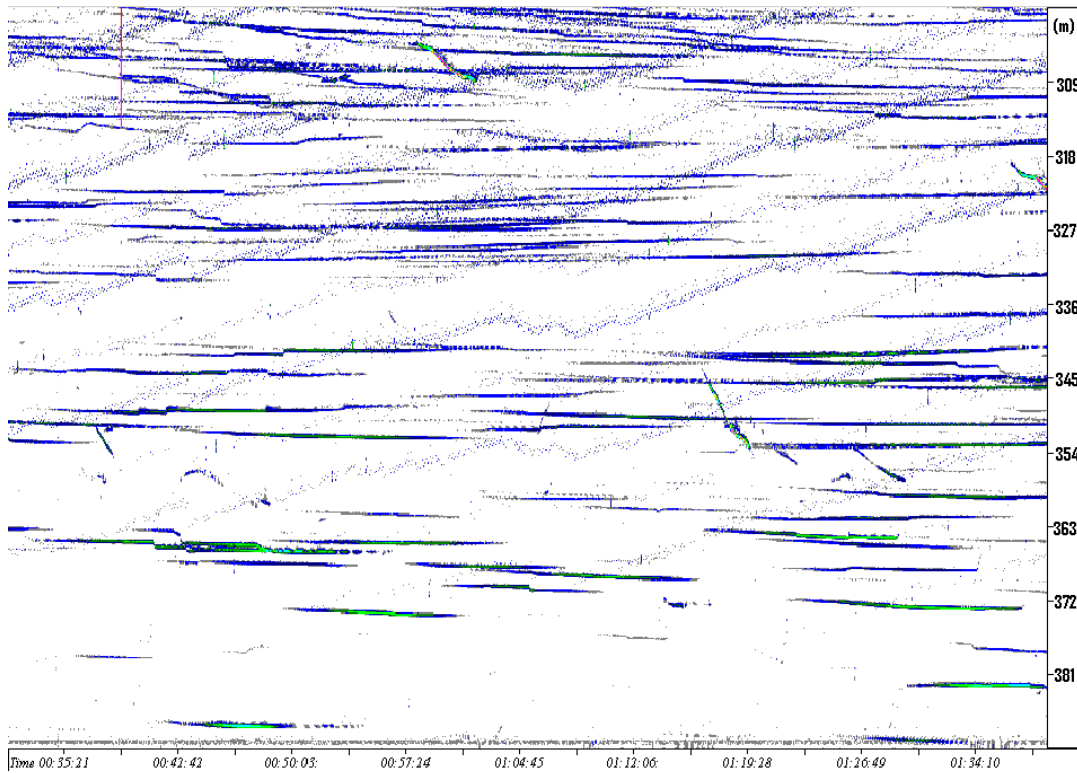
### 3.8.2 Close-ups at 300- 400 m

A closer look at the single targets at 300-400 m shows very little vertical movement during the day (Fig. 3.8.2.1) and at night (Fig. 3.8.2.2). They furthermore remained in the echo beam for a longer period which implies little net horizontal movement.

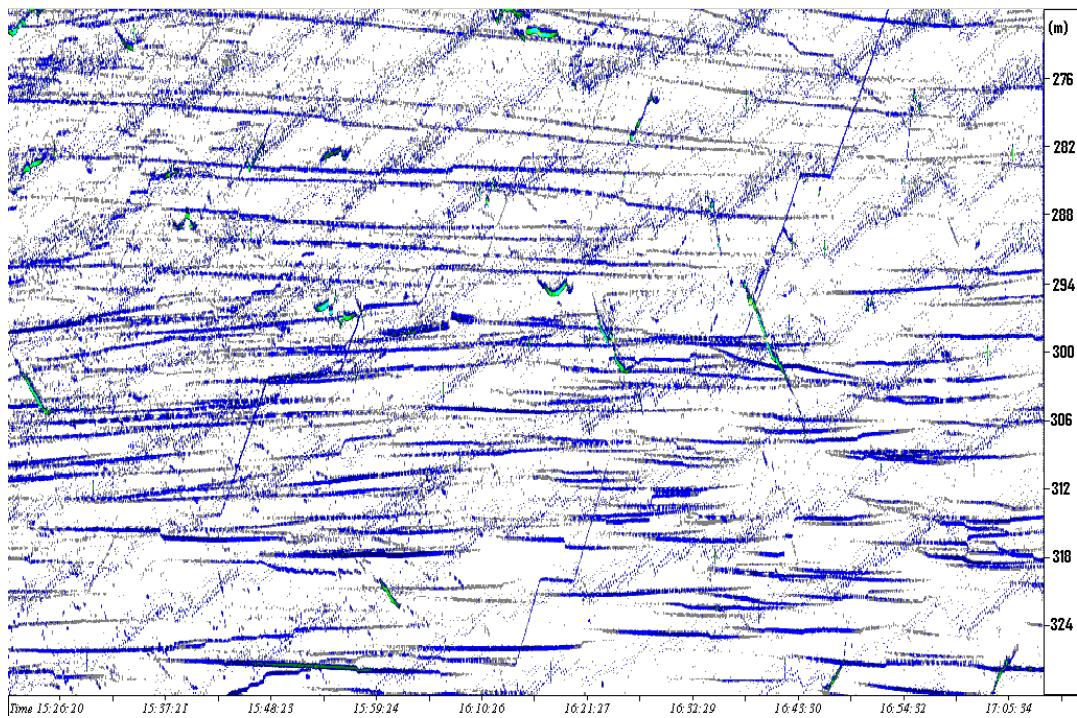
Just before the apparent sunset some targets were moving upwards in a step-wise pattern (Fig. 3.8.2.3). A few hours later downward moving targets were observed, descending both stepwise or in smoother tracks (Fig. 3.8.2.4). A few targets displayed more pronounced vertical swimming and could be ascribed to larger fish based on their TS ( $\sim 37$  dB). Downward moving targets were also observed during dawn, moving in a pronounced step-wise pattern (Fig. 3.8.2.5).



**Figure 3.8.2.1.** Echogram during day at 300-400 m.

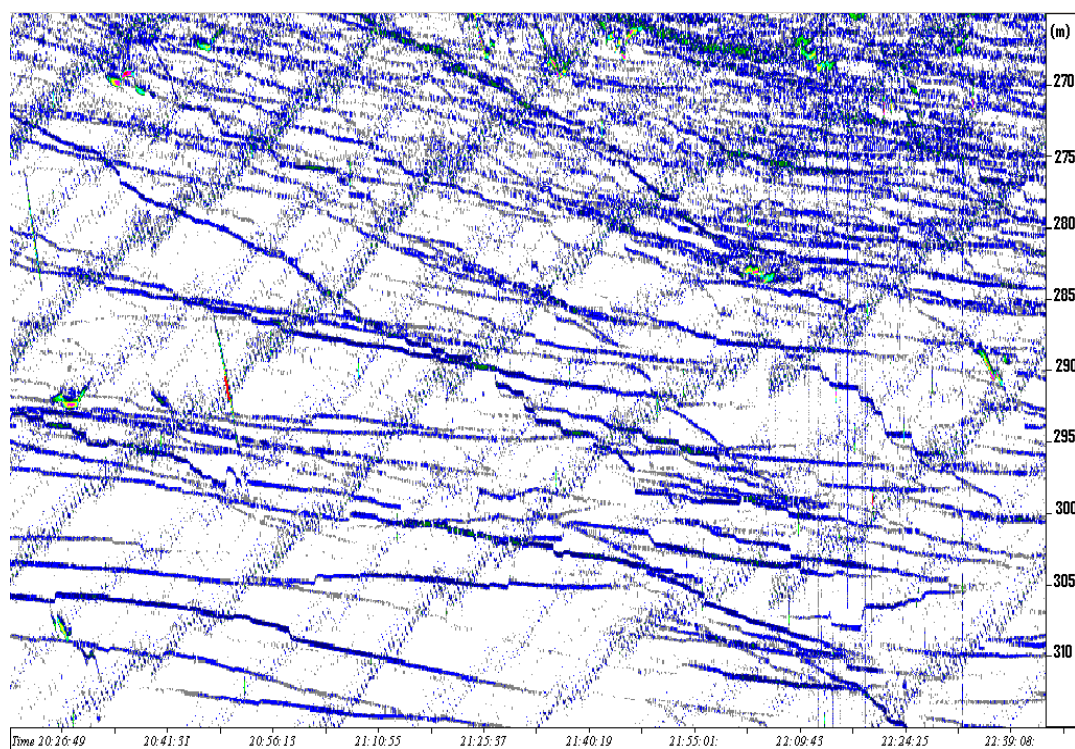


**Figure 3.8.2.2.** Echogram during night at 300-400 m.

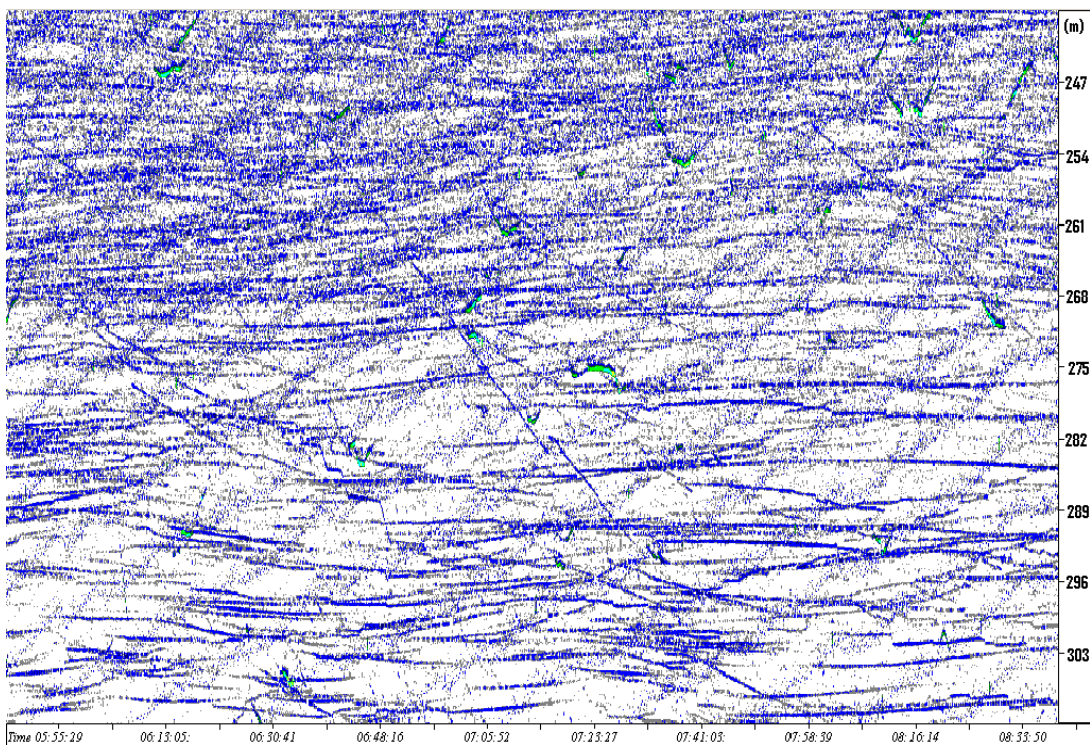


**Figure 3.8.2.3.** Echogram from 15:15 h to 17:20 h (GMT) at ~300 m depth.





**Figure 3.8.2.4.** Echogram from ~20:40 h to 23:40 h (GMT) at 300 m.



**Figure 3.8.2.5.** Echogram from ~06:40 h to 09:50 h (GMT) at 300 m.

### 3.8.3 Acoustic data analysis

#### *Automatic target tracking*

In total 5051 tracks passed the chosen filters. After separating the tracks into 4 time periods the numbers of tracks in the datasets were; Dawn = 690, Day=2032, Dusk= 553 and Night= 1478.

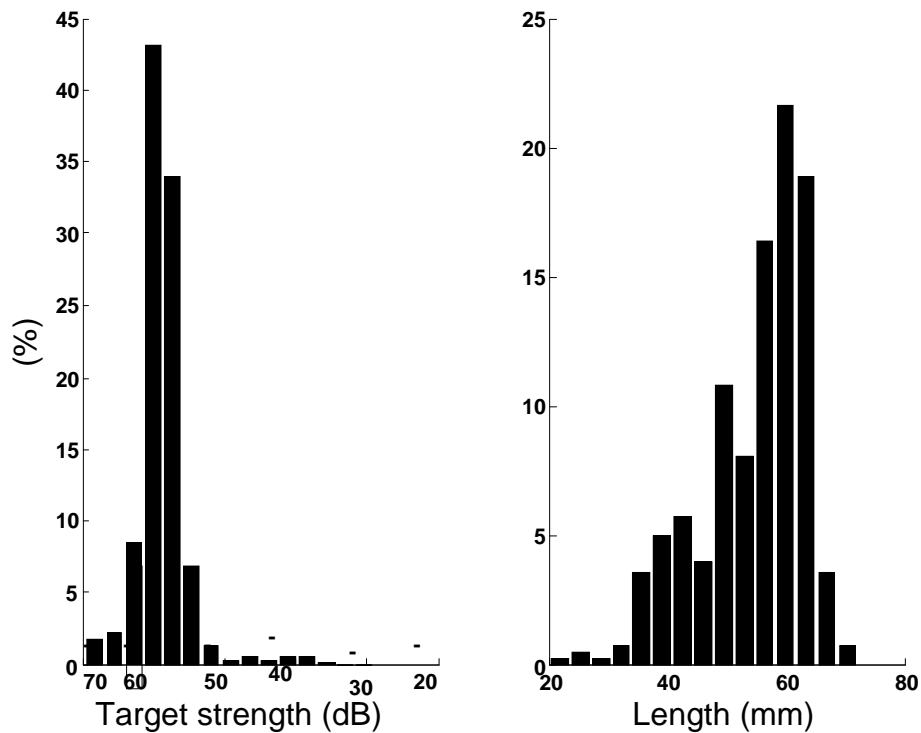
The track length varied between 10 and 1770 echoes with an average length of 66 echoes. The average target strength was -59 dB in all the time periods indicating that the species composition did not change with time.

#### *Target strength distribution*

The target strength distribution shows 2 groups. One group has a TS distribution in the range of -70 to -50 dB with a marked peak at ~-60 dB and is ascribed to mesopelagic fish. The much less frequently occurring group with TS > -50 is ascribed to larger fish.

The length frequencies of all the *B. glaciale* measured at 300-400 m peaked at 60 mm (Fig. 3.8.3.1) indicates that this is the length corresponding to a TS of -60 dB.

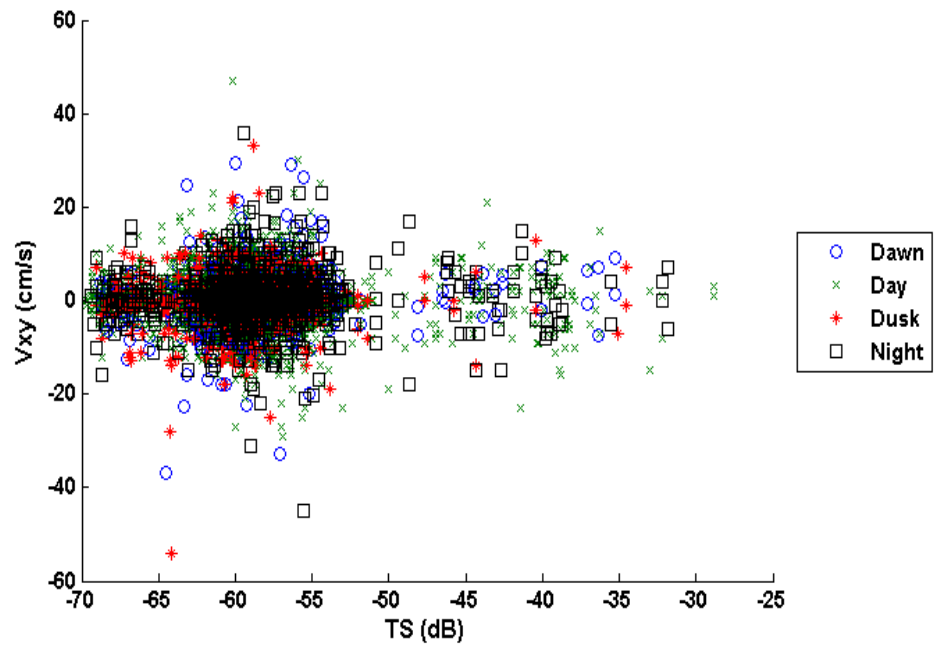




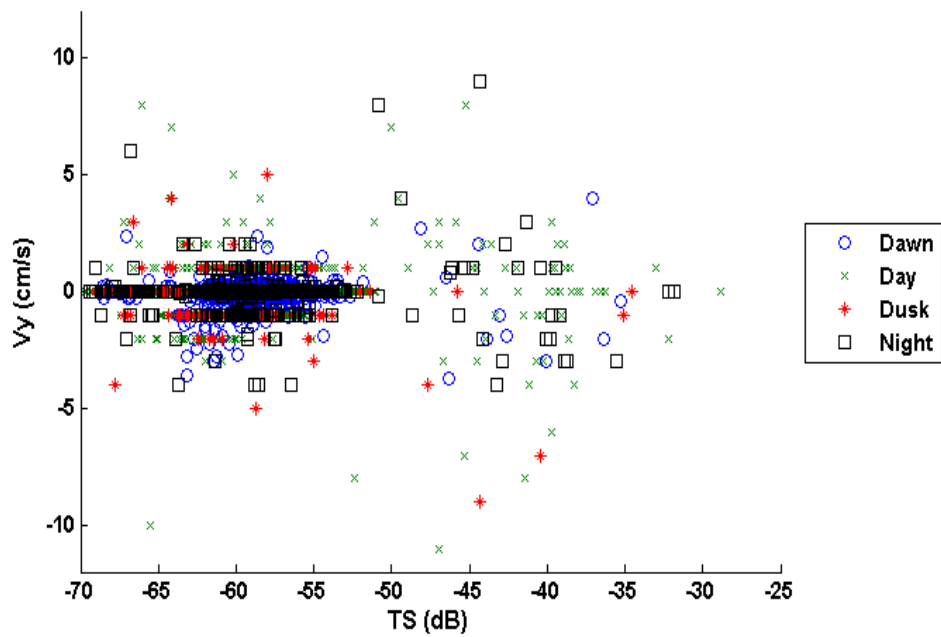
**Figure 4.8.3.1.** Targets strength distribution of all the tracks recorded during the 4 time periods (left). The length distribution of all the *B. glaciale* measured in 300-400 m (right).

### *Swimming velocities*

The analysis of swimming velocities did not reveal any difference between the time periods (Figures 4.8.3.2-3). The average absolute values varied from 2-3 cm s<sup>-1</sup> for the horizontal components with medians of -1,1 and 0. The vertical components had an absolute average value from 0.2-0.3 cm s<sup>-1</sup> for the vertical component median of 0 at all times.



**Figure 3.8.3.2.** The horizontal speed ( $\text{cm s}^{-1}$ ) components plotted against TS (-dB) for all the time periods.



**Figure 3.8.3.3.** The vertical speed component ( $\text{cm s}^{-1}$ ) plotted against TS for all the time periods.

### *Analysis of variations within tracks*

#### **Track 1**

The longest track recorded automatically lasted for 31 minutes and had 28 missing pings. The track was recorded during night and  $\sim 33.7$  m from the transducer. It had average TS at -63 dB and very little vertical ( $0.1 \text{ cm}^{-1}$ ) and horizontal movement ( $0.00$  and  $0.1 \text{ cm}^{-1}$ ). The SED echogram (Fig. 3.8.3.4) of the track shows that the target remained in the beam even longer, but the automatic tracker had divided the track into shorter fragments. The change in position and variation in speed and TS within the track are shown in figure 3.8.3.5. The speed was low with a short rapid movement. The variation in TS decreased with time and did not change with the variation in speed. There were a few rapid changes in vertical position during the track but not more than 20 cm. The largest changes in position correlated with the short rapid movement. The maximum speed was  $9.6 \text{ cm s}^{-1}$ .

### **Track 2**

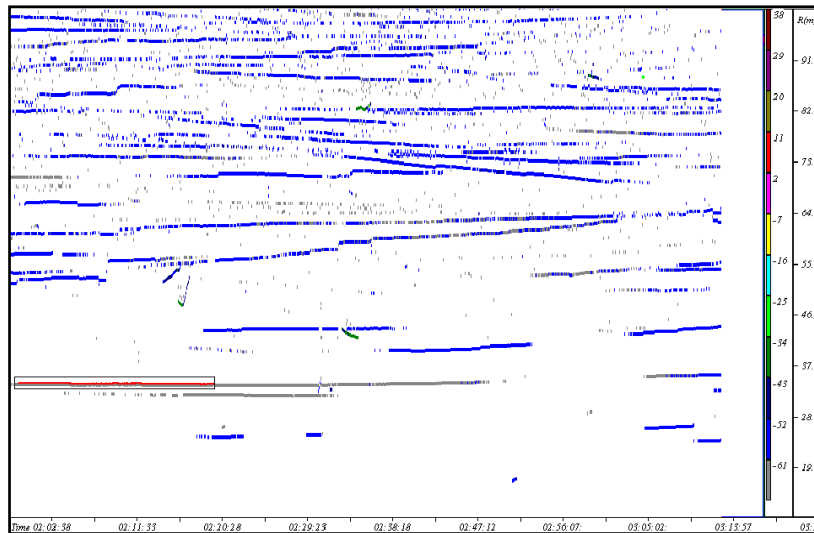
Track 2 was recorded at 19:00 h and ~15 m from the transducer. The track lasted for 6.5 minutes and is shown in figure 3.8.3.6. The TS varied in the range of -58.8 dB to -62.2 dB with average -60 dB (Fig. 3.8.3.7). The variation of speed within the track was similar both in pattern and values as in track 1. The highest speed was 12 cm s<sup>-1</sup> and the average was 2 cm s<sup>-1</sup>. The change in position shows also a more rapid shift in vertical position of ~ 25 cm.

### **Track 3**

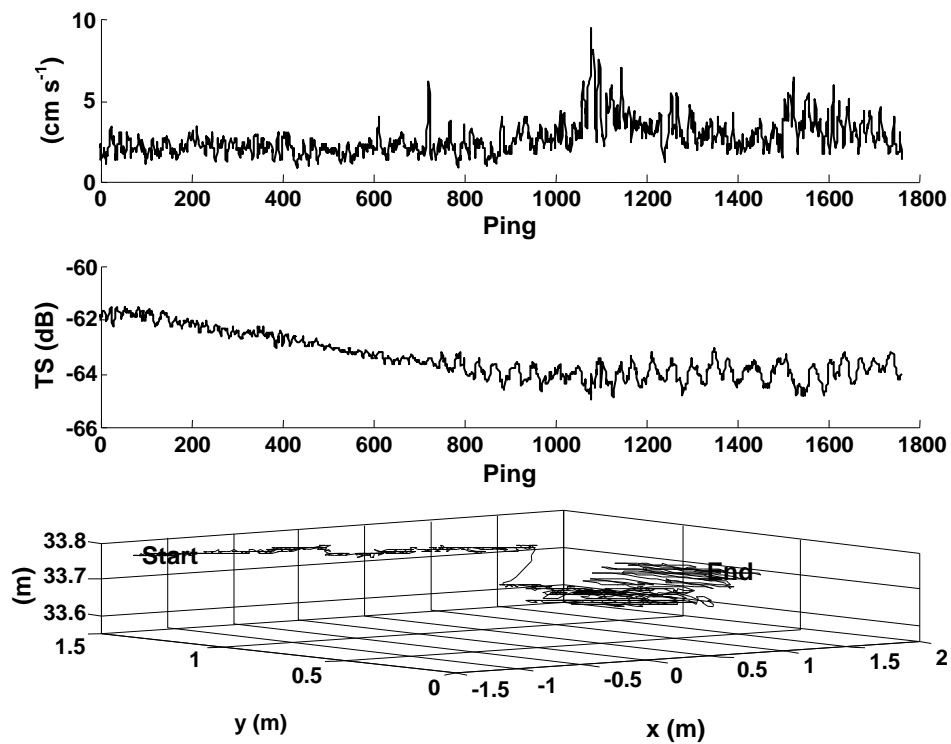
The track was 2.7 minutes long and recorded at 11:50 h at 16 m from the transducer (Fig. 3.8.3.8). The fish was slowly sinking during the track (Fig. 3.8.3.9). The speed varied frequently from 0 to ~ 4 cm s<sup>-1</sup>. Target strength varied from -61 db to -57 dB.

### **Track 4**

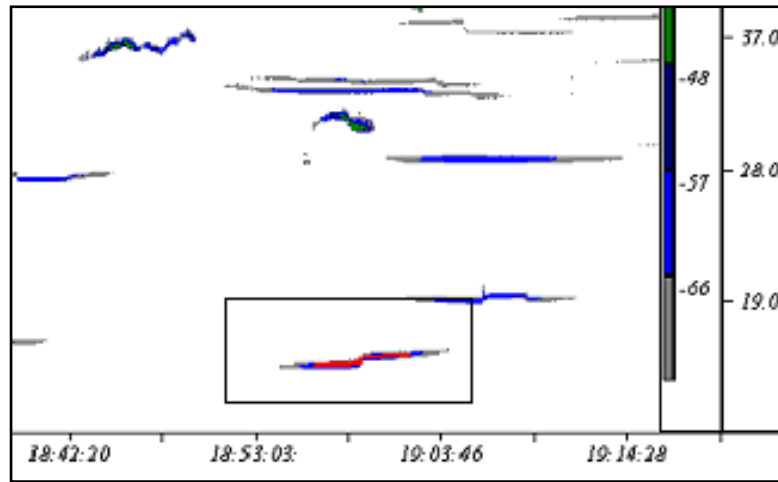
The track at 100 m (Fig. 3.8.3.10) from the transducer recorded at night was too far away to visualize a clear swimming pattern but moves within < 30 cm vertically and within a few meters horizontally (Fig. 3.8.3.11). It had average TS at -60 and varied from -64—58 dB. The track had 12 missing ping and lasted 9.3 min.



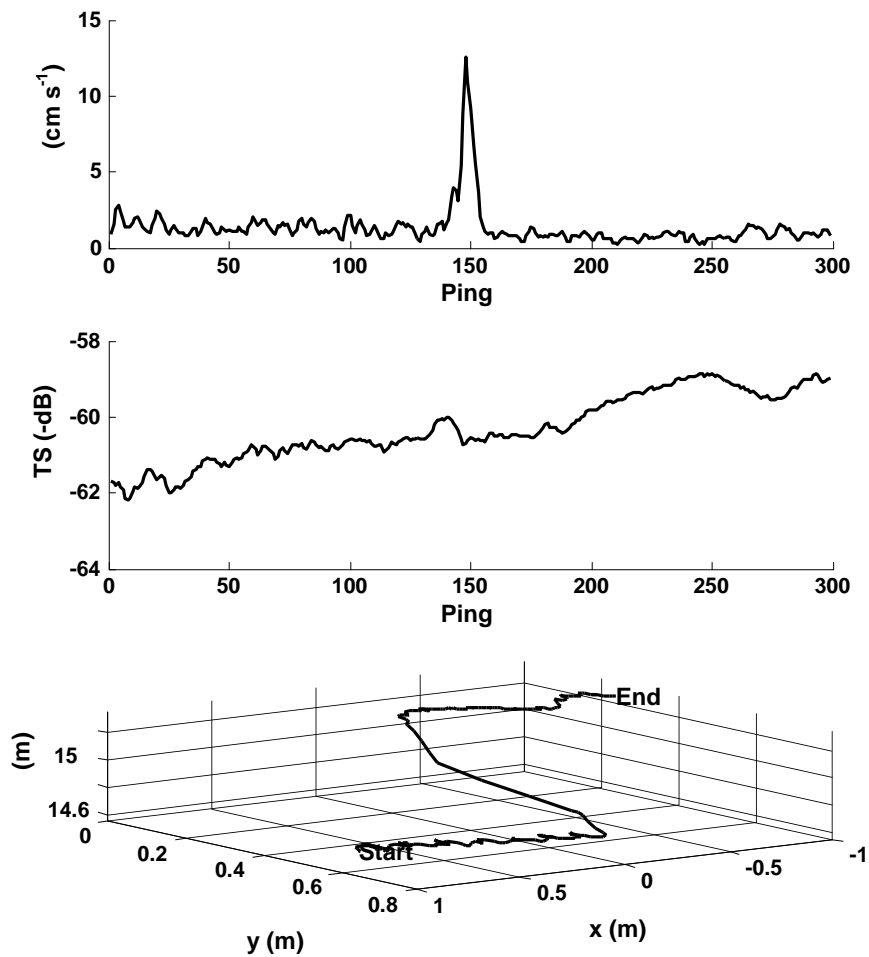
**Figure 3.8.3.4.** Echogram showing the longest track recorded (framed). The y-axis shows distance from the transducer and x-axis shows the time recorded (GMT).



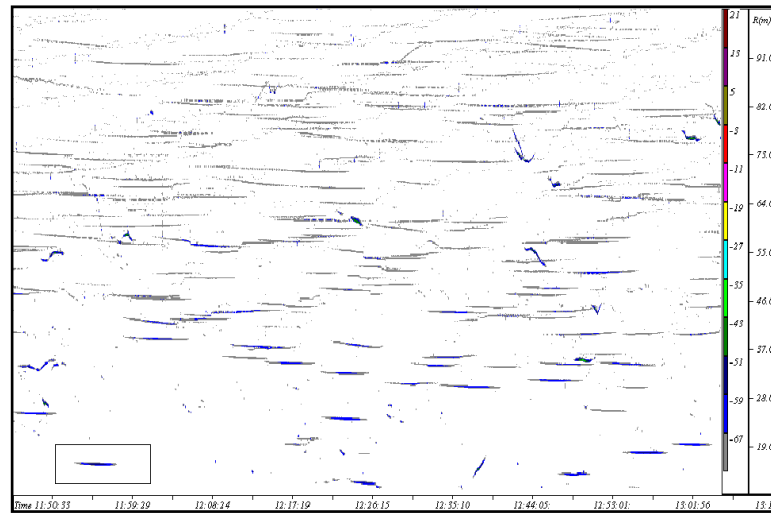
**Figure 3.8.3.5.** The variation in speed (upper), and TS (middle) and position (down) for the longest track, track 1, recorded by the automatic target tracker with distance from the transducer (z-axis).



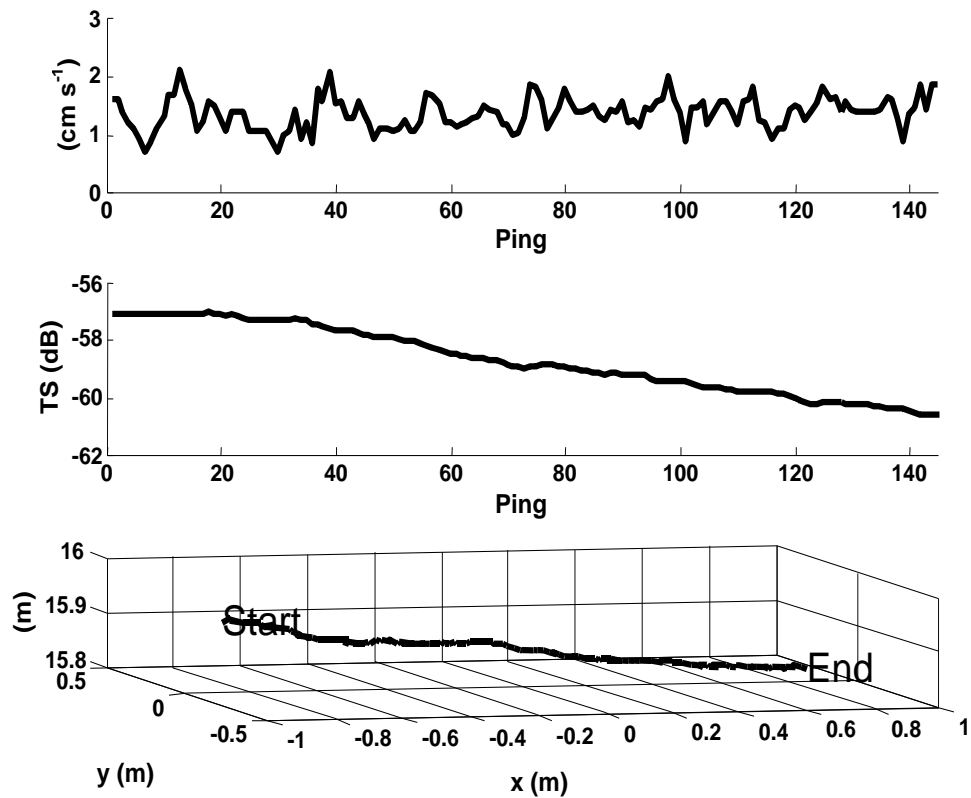
**Figure 3.8.3.6.** Echogram showing track 2 (framed). The y-axis shows distance from the transducer and x-axis shows the time recorded (GMT).



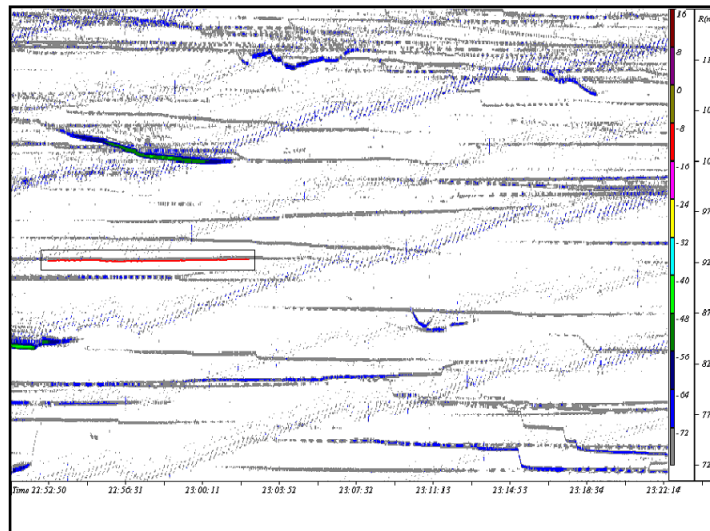
**Figure 3.8.3.7.** The variation in speed (upper), and Ts (middle) and position (down) for track 2 with distance from the transducer (z- axis).



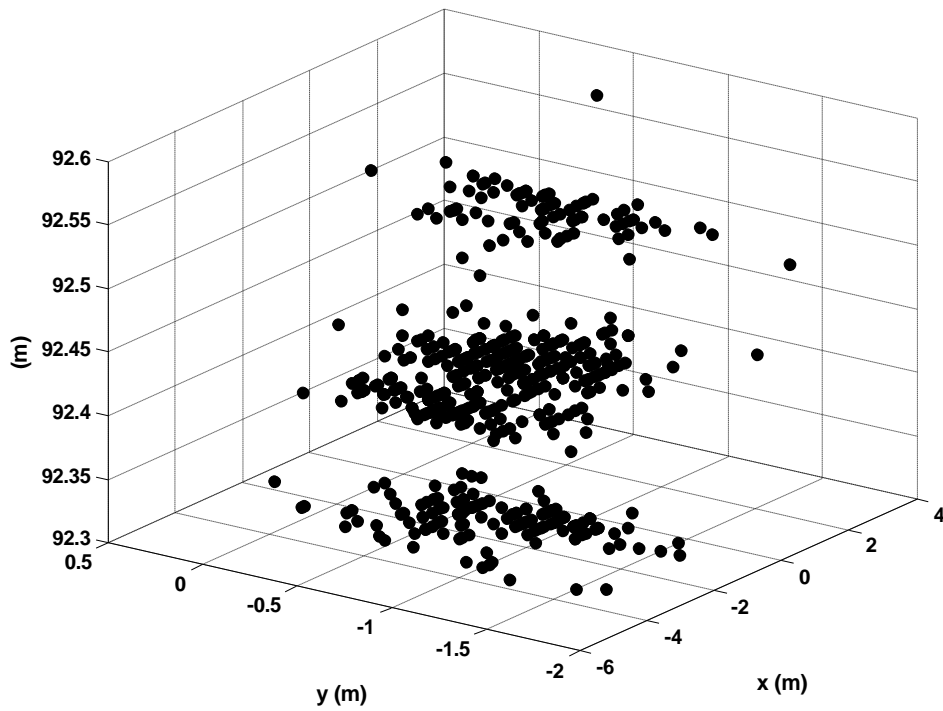
**Figure 3.8.3.8.** Echogram showing track 3 (framed). The y-axis shows the range from the transducer and the x-axis shows the time recorded (GMT).



**Figure 3.8.3.9.** The variation in speed (upper), TS (middle) and change in position (lower) of tack 3 with distance from the transducer (z-axis).



**Figure 3.8.3.10.** Echogram showing track 4 (framed). The y-axis shows the range from the transducer and the x-axis shows the time recorded (GMT).



**Figure 3.8.3.11.** The change in position of track 4 with distance from the transducer (z-axis).



## 4. Discussion

### 4.1 Mesozooplankton distribution

There was an unusually low abundance of mesozooplankton and in particular *Calanus* sp.. The concentration of *Calanus* sp. is normally found in one order of magnitude higher concentrations than in this study (Giske et. al., 1990; Baliño & Aksnes, 1993; Bagøien et al., 2001). No detailed species identification was carried out, the species *C. finmarchicus* was recognized but other species can not be excluded. In Masfjorden *C. finmarchicus* is normally dominant but *C. helgolandicus* is also present (Bagøien et al., 2001).

There was not time for sampling mesozooplankton both day and night, but any changes in vertical distribution from day to night are considered to be of less importance in this study for the following reasons. The main concentration of copepods occurred in the upper 50 m even at day, overwintering *Calanus* do not perform DVM, while *Metridia* and *Chiridius* are known to move towards the surface at night (Baliño & Aksnes, 1993). The two latter species did, however, occur in very low numbers and are expected to have little influence for the distribution of *B. glaciale*.

### 4.2 Vertical distribution and migration pattern

The species occurred in discrete depth layers. Euphausiids were not identified to species but are assumed to be *Meganyctiphanes norvegica*, which is the prevailing species in the fjord. The prevailing pelagic shrimps are *Sergestes arcticus* and *Pasiphaea multidentata* (Kaartvedt et al., 1988, Giske et al., 1990).

The highest catches of *B. glaciale* during day were at 100-200 m, though the actual highest concentrations based on the acoustic data appear to occur at the lower SL at 180-230 m with a possible peak in concentration at ~200 m. At night, about 60% of the population of *B. glaciale* stayed above 100 m while 30 % remained below 200 m.

Light is assumed to be the most important cue to trigger DVM, acting as a controlling and orienting factor (Forward, 1988; Baliño & Aksnes, 1993) resulting in a synchronous migration pattern of a population (Pearre, 2003). However, when the main purpose for conducting DVM is to feed, a starvation signal or a satiation signal may induce or obstruct vertical migration. This may cause an asynchronous migration pattern within a population and even a bimodal vertical distribution of the population during night (Pearre, 2003).

No indications of an asynchronous migration pattern were seen within the population of *B. glaciale* in the period studied. In the echograms up-ward moving targets were observed only at dusk with a part of the population remaining at depth even during the night.

The sequential horizontal tows at sunset collected species during DVM to upper layers. The species appeared in the trawl in a time sequence resembling the vertical distribution during the day.

The lower, weaker backscattering layer had a pattern similar to that of the upper SL; a rise at dusk, followed by a midnight-sinking and a dawn rise. Swimming deeper after a resident time at the surface is termed midnight-sinking (Pearre, 2003). In the case of midnight-sinking by *M. muelleri*, this has been explained by the use of an “anti-predation window” (Giske et al., 1990; Giske & Aksnes, 1992, Baliño & Aksnes, 1993). The periods at dusk and dawn represent a window in time when the light is strong enough to forage while sufficiently low to reduce risk of predation (Clark & Levy, 1988).

The behaviour of the *B. glaciale* in the lower SL is unclear as is the importance of light in feeding. As light decreases, new more shallow foraging grounds may become available, i.e. representing deep anti-predation windows during the dusk and dawn. As the low light disappears, individuals may also sink back to avoid predators, even in the darkness of night.

The temperature was more or less constant, below 75 m, excluding temperature as an explanation for distributions in deep water.

*Maurolicus muelleri* appeared in noteworthy numbers in the catches from tows at 300-400 m both day and night compared to results from Kaartvedt et al. (1988) and Giske et al. (1990), but with large variations between the tows. Their number was low compared to the high concentrations at upper layers, but high or as high compared to the amount of *B. glaciale* at 300-400 m (c.f. Tab. 3). There was no correlation with time (day or night) and frequency of individuals. More shallow tows, capturing large amounts of *M. muelleri* were carried out before 3 of the 4 deep tows, pointing to the possibility of some contamination from previous sampling. It is not possible to conclude that all the targets seen in the echogram at 300-400 m are *B. glaciale*.

### 4.3 Length distributions

Gjøseter (1973a) found the average length for the age groups 0-5 to be; 20 mm, 38 mm, 48 mm, 60 mm, 65 mm and > 70 mm. The length distribution figure shows all the age groups present and peaks that correlate with Gjøseter's result. Mortality would expectedly lead to a reduction in number by age, but instead, 60 mm fish representing age group 3 dominated. This may be caused by the sampling method as small fish possibly manage to escape through the trawls net. Fish were only sampled in one part of the fjord, and it is also possible that different age groups have different horizontal distribution.

During the day a few specimens were found in the illuminated upper layer at 0-100 m. They were small and no representatives of the dominant age group 4 were present. The number of small fish decreased with depth with older individuals becoming more common in the 2 deepest intervals. Although no significant difference was recorded, size distributions by depth agreed with previous studies of *B. glaciale*, showing tendencies of increasing length with depth (Halliday, 1970; Sameoto, 1988). Smaller *B. glaciale* accordingly appeared before larger specimens in the sequential tows after sunset (c.f. Fig. 3.6.2).

## 4.4 Stomach analysis

*Benthosema glaciale* were mainly feeding on *Calanus* sp. despite its low abundance, and on *Metridia* sp., *Chiridius* sp. and ostracods in correlation to their proportion in the zooplankton sample. Only a few smaller copepods were found, supposedly *Micro-* or *Paracalanus*. The rather abundant *Acartia* sp. and *Oithonia* sp. were not observed in any stomachs. This might be due to a negative selection for these species and smaller copepods. Sameoto (1988) found a negative selection for prey < 1 mm. Gjørøster (1973b) reported that *B. glaciale* prefer the large copepods; *Calanus finmarchicus*, *Metridia* sp. and *Pareuchaeta norvegica* but were also feeding on euphausiids in Norwegian fjords.

*Acartia* spp. and *Oithona* spp. were mainly concentrated at 0-50 m and only 5 fish were collected at this depth during the day. The fish collected at this depth during the night contained little fresh, identifiable stomach content. Smaller prey are assumed to be digested and evacuated from the stomachs faster than larger prey (Jobling, 1981), which may influence the possibility of identifying these copepods in the stomach content.

Euphausiids and sergestiid shrimps might be important preys in addition to copepods as their size imply that they contribute much more in terms of biomass than in terms of numbers. Gjørøster (1973b) suggested that the importance of euphausiids might be seasonal and increase when the abundance of *Calanus* is scarce. The fish that had fed of euphausiids and sergestiids were mainly collected at deeper waters with the highest proportion at 300–400 m (~18 % during day and 13% during night). Euphausiids were concentrated at 100-200 m during day but appeared in the trawl at all depths. One *B. glaciale* collected at 100-200 m during day had obviously fed recently with one fresh euphausiid in the stomach. Although, most of the euphausiids in the stomach content were often much digested and sometimes only larger segments and eyes were found. No documentation exists in literature concerning the rate of digestion and gastric evacuation of *B. glaciale* and it cannot be excluded that the

euphausiids in the stomach content were the remains from a feeding period at the surface on a previous night.

This study shows evidence of both day and night feeding. Previous studies show that *Benthosema glaciale* feeds mainly at night after migrating to shallower waters but there is also evidence of daytime feeding (Sameoto, 1988, 1989; Gjørseter, 1973b; Bagøien, 2001). Sameoto (1988) recorded the most intensive feeding period at night off the Nova Scotia shelf. Gjørseter (1973b) found slight diurnal feeding activity with higher frequency of full stomachs in the evening, 2 hours after sunset in Byfjorden and Herdlefjorden.

This study covered a time period from 11:00 h to 22:30 h and thus only the first few hours of darkness. *Benthosema glaciale* in Masfjorden might continue feeding later in the night. The higher frequency of more full stomachs during day may be the result of night or dawn feeding since there were few stomachs with fresh content. The state of digestion increased during the day, which would be expected after a period of night/dawn feeding.

The stomachs examined from fish in the horizontal trawls and of the non-migrating population showed little difference, although fish at depth had a slightly higher frequency of empty stomachs. Feeding may occur at depth even later than at dusk since fresh content was found several hours after sunset.

An important source of error when conducting stomach analysis of fish is the possibility of feeding inside the trawl or regurgitation of food after capture. Only one fish had stomach content in the oesophagus, one slightly digested euphausiid. The fact that there was little fresh stomach content found indicates that the fish did not feed in the trawl. It is therefore concluded that trawl feeding and regurgitation are of little importance in this study.

## 4.5 Acoustical data analysis

### 4.5.1 Target strength

The TS varied from -50 to -70 dB with a peak at -60 dB for the group containing mesopelagic fish. The same TS distribution was found for *M. muelleri* and *B. glaciale* in Sør fjorden by Torgersen & Kaartvedt (2001) and the 2 species cannot be separated by differences in target strength.

Variation in TS is dependent on the tilt of the body and is thereby sensitive to vertical swimming speed and direction (Røstad, 2006). Fish has its maximum TS when the swim bladder is perpendicular to the transducer, but a small change in tilt angle may easily reduce the TS with 20 dB for a gadoid fish (Foote, 1980). The TS varied with ~ 3-4 dB within the tracks, i.e. from ping to ping, for the tracks analysed, indicating little tilting of the body. The TS was higher when the fish was furthest away from the transducer. The tracks showed rapid shifts in vertical position but this did not seem to affect the target strength, since no change in TS recordings occurred. *Benthosema glaciale* have little gas in their swim bladder (Kaartvedt et al., unpublished) and the target strength might be less sensitive to tilting of the body.

### 4.5.2 Swimming speed and behaviour

The majority of the tracks in the group of mesopelagic fish had none or low swimming speeds,  $< 5 \text{ cm s}^{-1}$  for the horizontal components and even less for the vertical component,  $< 1 \text{ cm s}^{-1}$ .

The ecological implication is that the majority of the fish in the lower water column had little or no activity. Several studies have shown that food intake and swimming velocities are closely linked and speeds less than one body length, BL, per second are considered to be routine swimming (no foraging) and demands little energy (Videler, 1993). Some tracks had a higher horizontal swimming speed of  $> 10 \text{ cm s}^{-1}$ . They can possibly represent search behaviour since feeding evidently occurred at this depth. *Benthosema glaciale* are considered to be an opportunistic feeder and can probably switch swimming behaviour, from a low energy-demanding mode, to a foraging

behaviour. Small fish can have a maximum sustained speed of  $3 \text{ BL s}^{-1}$  with burst speeds of  $7 \text{ BL s}^{-1}$  (Videler, 1993) and speeds higher than  $> 50 \text{ cm s}^{-1}$  are not realistic.

Tracks studied in more detail had in common a low swimming speed, less than  $1 \text{ body length s}^{-1}$ , yet with frequent changes in speed. The behaviour may simply be due to 1 or more beatings of the tail, followed by a glide. Such swimming behaviour has been observed in the Cape anchovy, *Engraulis capensis* during normal swimming with no feeding (James & Findlay, 1989).

Tracking far from the transducer can result in quite large deviation in horizontal position. Still, also tracks at 100 m range had little movement, as all the position detections are centred within a small area (c.f. figure 3.8.3.11).

Rapid vertical changes were also seen in the echograms at 300-400 m. The tracks were usually long, appearing as a straight line, with intermittent changes in vertical position. It is possible that a rapid shift in vertical position represents a search behaviour (c.f. O'Brien et al., 1990). They argued that fish search behaviour may display a distinctive pattern of stops and starts in which pauses to search for prey alternate with reposition for the predator for scanning new territory. Such stop-and-go behavior is termed saltatory search. The saltatory search can be varied to suit local environmental conditions such as prey concentration and prey size. The observed shifts in vertical positions may represent a shift in territory. The pronounced step-wise pattern observed at dusk (c.f. figure 3.8.2.3) concurs with saltatory search. However, observations by submersibles (Barham, 1971) unveiled that myctophiids were swimming in a step-wise pattern also during escape so that this type of behaviour may have more than one explanation.

## **Validity of the data**

Sources of error when conducting automatic target tracking comprise the risk of recording of non-existing tracks, and breaking one track into shorter fragments.

The probability of the software adding single echoes into a non-existing track is higher when the density of echoes is high. The density of targets was low but increased with range. Echograms showed clear visual tracks. The filters in the automatic target tracking were quite strict which increased the possibility of breaking up the tracks in into one or more fragments. This evidently happened in track 1.

When the range increased and density of targets increased, non-existing tracks may have been recorded. This could result in tracks with high speed.

Measured swimming velocities will be biased, increasing with range from the transducer since target positions becomes less accurate (Røstad, 2006). No smoothing was carried out to avoid this problem and this may also have affected the very high computed horizontal speeds.

Even if a few invalid tracks were recorded, this is assumed to have little influence on the overall TS and speed distribution.



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